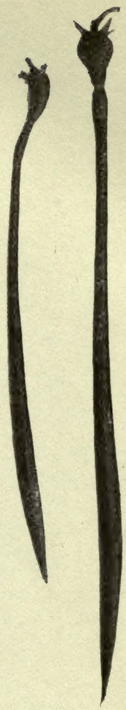
OBSERVATIONS OF A NATURALIST IN THE PACIFIC BETWEEN 1896 AND 1899

[*Frontispiece*

Selala (Vanua Levu, Fiji) ($\frac{1}{3}$).



Fruits with seedlings nearly ready to fall from the tree o
Rhizophora mangle (shortest) and Rhizophora mucronat
(longest). From Vanua Levu, Fiji. ($\frac{1}{4}$ of the tru
length.)

Rhizophora mangle (Vanua Levu, Fiji) ($\frac{1}{4}$).

Rhizophora mucronata (Vanua Levu, Fiji) ($\frac{1}{5}$).

OBSERVATIONS OF A NATURALIST IN THE PACIFIC BETWEEN 1896 AND 1899

BY

H. B. GUPPY, M.B., F.R.S.E.

VOLUME II

PLANT-DISPERSAL

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Dedication

TO THOSE NUMEROUS PERSONS TO WHOM I WAS INDEBTED FOR GREAT KINDNESS AND ASSISTANCE DURING MY SOJOURN IN HAWAII AND FIJI

PREFACE

ALTHOUGH this volume contains a great amount of original material, I am largely indebted to the labours of my predecessors for its present form; and a scheme that at first was limited only to my own observations in the Pacific has gradually extended itself to the general subject of plant-dispersal. The farther I proceeded in my work the more I realised that the floras of the Pacific islands are of most interest in their connections, and that the problems affecting them are problems concerning the whole plant-world. Deprived of the writings of Seemann, Hillebrand, Drake del Castillo, and other botanists, several of whom have lived and died in the midst of their studies of these floras, and without the aid of the works of Hemsley and Schimper, generalisers who have mainly cleared the way for the systematic study of plant-distribution and plant-dispersal, it would not have been possible for me to accomplish such an undertaking.

My interest in plant-dispersal dates back to 1884, when, whilst surgeon of H.M.S. *Lark*, in the Solomon Islands, I made some observations on the stocking of a coral island with its plants, which were published in the *Report on the Botany of the "Challenger" Expedition*. In 1888 I followed up the same line of investigation during a sojourn of three months on Keeling Atoll, and during a journey along the coasts of West Java. But realising that as yet I had barely touched the fringe of a great subject, and that several years of study would be required before one could venture even to appreciate the nature of the problems involved and much less to weigh results,

I took advantage of the circumstances of my life to make, between the years 1890 and 1896, a prolonged investigation of the plants of the British flora, mainly from the standpoint of dispersal by water. This involved the study of the seed-drift of ponds and rivers and of the plants supplying it, a study which brought me into close relation with aquatic and sub-aquatic plants. This line of investigation led me into contact with many other aspects of plant-life; and as time went on my field of interest extended to the plants of dry stations and to the bird as an agent in plant-dispersal. Only a few of these results have been published, as in the journals of the Linnean Society and of the Royal Physical Society of Edinburgh as well as in the pages of *Science Gossip*. They lie for the most part still within my note-books, and fitly so, since I regarded such studies chiefly as a preparation for the investigation of the general question of plant-dispersal.

When again, in October, 1896, I found myself once more in the Pacific, the subject was taken up again with zeal; but my larger experience had only increased my diffidence, and the unknown looked so overwhelming that I settled down for the next three years content with merely making experiments and recording observations. Here again the main problem was attacked through the study of seed-buoyancy, and gradually it led me to the systematic study of the mangroves and of the beach-plants, whilst my inland excursions brought me into familiarity with the plants of the interior. My geological exploration of the island of Vanua Levu, in Fiji, greatly assisted me by giving a method to my botanical examination of the island.

Whilst working out my geological collections in England, in the years 1900–1902, I devoted an hour or two daily to the elaboration of my botanical notes and to a consideration of the problems concerned. During a winter in Sicily I took up again the subject of the beach-plants; and after the publication of the volume on the geology of Vanua Levu I was able to accomplish a plan, for years in my dreams, of visiting the eastern shores of the Pacific. During a period of three months

from December, 1903, to March, 1904, I examined the littoral flora of the west side of South America at various localities between Southern Chile and Ecuador; and finally completed this investigation by comparing the shore-plants on the Pacific and Atlantic coasts of the isthmus of Panama. Returning to England with a fresh collection of data, I passed many months in elaborating and arranging all my notes, waiting vainly for a clue to guide me in framing a scheme by which I could bring the results of many years of work into some connected form. At last I decided once again to take the floating seed as my clue, and without any prearranged plan I allowed the work to evolve itself. Now that it is finished, I can see some obvious defects; but if any other plan had been adopted I scarcely think that I should have been more successful in piecing together in a single argument materials resulting from so many years of research and relating to so many aspects of plant-life.

Yet the final object of a naturalist would be but a sorry one, if his aim were only to write a treatise and append his name to it. His personal faith lies behind all his work; and no one can pursue a long line of study of the world around him without rising from his task with some convictions gained and some convictions lost.

As far as the observation of Nature's processes at present in operation can guide us, the world presents itself to us only as a differentiating world. We can perceive, it is true, a progressive arrangement of types of organisms from the lowest to the highest, and we can perceive a development of varieties of the several types; but the only process evident to our observation is that concerned with the production of varieties of the type. Nature does not enlighten us as to the mode of development of the type itself. We can, for instance, detect in actual operation the process by which the different kinds of bats or the different kinds of men have been developed; but there is no principle in Nature evident to our senses that is concerned with type-creation. Though we can supply it by hypothesis, we cannot discover it in fact. On the other hand, the evidence of differentiation is abundant on all sides of us, both in the organic and in the inorganic worlds. The history

of the globe has ever proceeded from the uniform to the complex; and in the closing chapter of this book an endeavour is made to connect the differentiation of plant and bird with the differentiation of the conditions of existence on the earth. But this leaves no room for the development of new types of organisms; and so far as observation of the processes of Nature at present working around us can guide us, each type might well be regarded as eternal. We can never hope to arrive at an explanation of the progressive development of types by studying the differentiating process; and since the last is alone cognisable for us, evolution, as it is usually termed, becomes an article of our faith, and of faith only.

In illustration of this argument, let me take the case of the races of men. We see mankind in our own day illustrating the law of differentiation all over the globe, as far as physical characters are concerned. Just as the ornithologist would postulate a generalised type in tracing the origin of various allied groups of birds, so the anthropologist, guided by his observation of the changes now offered by man in different regions, would postulate a generalised original type as the parent-stock of mankind. Observation of the processes of change now in operation by no means leads us to infer that such a generalised type was an anthropoid ape, or even simian in character. In so doing we should be forming a conclusion not warranted by the observation of existing agencies of change, and we should be confusing the two distinct processes of evolution and differentiation, or rather of progressive and divergent evolution, of which the last alone comes within our field of cognition. The study of variation can do no more than enable us to ascertain the mode of development of different kinds, we will say, of birds or of men. The origin of the type lies outside our observation. "Given the type, to explain its origin": this is the problem we can never solve, and Nature aids us nothing by the study of her ways. On the other hand, there is the subsidiary problem . . . "Given a type, to explain its varieties" . . .; and here Nature's processes are apparent to us in a thousand different shapes.

It might seem that the presumptive evidence connecting man in his origin with the monkeys is so strong that, supposing his

simian descent were regarded as a crime, a jury would without hesitation pronounce his guilt; but until some observer of the processes followed by Nature can bridge over the gap that divides man from the ape, until indeed he can offer a legitimate illustration of how it is accomplished in similar cases in our own day, the gap remains. Those who have read the recent work of Prof. Metchnikoff on the Nature of Man will properly regard his chapter on the simian origin of man as a brilliant argument advanced by a most competent authority. Yet he fails to complete his case by bridging over this gap, and can only appeal to the results of the now famous researches of De Vries concerning the mutations of the evening primrose (Œnothera). It is probable, he says, that man owes his origin to a similar phenomenon (English edition, p. 57). Several objections could be raised against this illustration from the plant-world, the most important of them lying in the circumstance that these mutations could only be urged as instances of the sudden development of new species of the evening primrose type. They merely illustrate the process of differentiation from a given type, and by no means represent the process of progressive evolution from a simian to a man.

However, look where we may—and this is the great lesson I have learned from my researches in the Pacific islands—Nature does not present to our observation any process in operation by which a new type of organism is produced. The processes involved lie hidden from our view. The channels by which impressions from the outside world reach us are comparatively few; and although it seems likely that the future development of man will be mainly concerned with the acquirement of additional sense-channels, no newly acquired sense will enable him to be at once an actor in and a spectator of the great drama presented in the organic world. That a creature should be able to get at the back of its own existence, or, in other words, to penetrate the secret of its own creation, is unthinkable. Outside the limited field of observation that immediately surrounds us extends the region where reason alone can guide us, and beyond lies the realm where reason fails and faith begins.

H. B. GUPPY.

November 8th, 1905.

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ADDITIONS AND CORRECTIONS

Page 5 and subsequent pages. *For* Ipomea *read* Ipomœa.

,, 68. *For* Hippomanes *read* Hippomane.

,, 68. *For* Conocarpus erecta *read* Conocarpus erectus.

,, 122. Sir W. Buller includes the fruits of the Puriri tree (Vitex littoralis, according to Kirk) amongst the food of the New Zealand fruit-pigeons.

,, 177. *For* Entata, in the head-line, *read* Entada.

,, 266. The fruits of Oncocarpus vitiensis have been found in the crop of a Fijian fruit-pigeon (Carpophaga latrans). *See* Hemsley's *Bot. Chall. Exped.*, Introd., 46, and iv. 308; also Newton's *Dictionary of Birds*, p. 724.

,, 368. Sernander (p. 185) observes that the fruits of Naias marina have little or no floating power.

,, 416. For the first eight lines read as follows :—"Of these, 22 occur in Continental regions on both sides of the Pacific; 12 are found in the Old World alone; one is peculiarly American, and two are confined to the Australian and Polynesian regions. A few of these can be regarded as exclusively American in their origin, though the bulk of them hail evidently in the first place from the Old World. But from the circumstance that all or most of the other species of the genus concerned are confined to America, it may legitimately be inferred that Waltheria americana, Ageratum conyzoides, and Physalis angulata are American-born species. Teucrium inflatum is a peculiar instance of an American weed collected in Polynesia before apparently it had been recorded from the Old World."

,, 417. Add after Cardiospermum halicacabum. . . . . "Its seeds, as my experiments show, possess little or no capacity for dispersal by currents, since they sink at once or within a few days, even after drying for months."

,, 455. Omit the reference to figure 6 in the centre of the page.

,, 498. *For* Conocarpus erecta *read* Conocarpus erectus.

,, 498. *For* Hippomanes *read* Hippomane.

,, 508. Amongst my Solomon Island collections identified at Kew were the fruits of a species of Litsea from the crop of a fruit-pigeon (Hemsley's *Bot. Chall. Exped.*, IV. 295.

,, 533. *For* Commelyne *read* Commelina.

,, 539. At foot of page, *for* Thames sea-drift, *read* Thames seed-drift.

,, 581. *For* Crambe maritimum *read* Crambe maritima.

,, 618. Under Mascarene Islands add Myoporum to the plants linking them to the Pacific Islands.

OBSERVATIONS OF A NATURALIST IN THE PACIFIC

CHAPTER I

INTRODUCTION

The study of insular floras.—Their investigation in this work from the standpoint of dispersal.—The significance of plant-distribution in the Pacific.—The problems connected with the mountain-flora of Hawaii.—The persistence of dispersing agencies at the coast, their partial suspension on the mountain-top, their more or less complete suspension in the forest, and the effect on the endemic character of plants.—The connection between the endemism of birds and plants.—The relative antiquity of plants of the coast, forest, and mountain-top.—The genetic relation between coast and inland species of the same genus.—The ethics of plant-dispersal.—Evolution takes no heed of modes of dispersal.—The seed-stage is the price of Adaptation.

TO proceed from the general to the special is the only method of dealing with insular floras. A broad and comprehensive grasp of plant-distribution, such as is only acquired by a life-time of research aided by travel and the handling of large collections, is a necessary foundation for the study; yet in the nature of things such qualifications can be possessed by but a few. To direct an inquiry in the opposite direction, and endeavour to attack the problem of continental floras through the insular floras would result merely in the investigation of a few of the many questions connected with plant-distribution.

The panoramic sketch of the surveyor on the mountain-top aids him in a thousand ways when after months of tedious labour he plots the details in his chart. Without such a panoramic view of the plant-world in his mind's eye, an observer like myself can only look for guidance to the writings of those who have

generalised on the foundations of a far broader experience, such as those of Bentham, De Candolle, Gray, Hooker, Schimper, and others.

It would be quite possible for a botanist possessing a profound general acquaintance with the plant-world to dispense altogether with actual observation and experiment on modes of dispersal. It would be quite possible for him to arrive at conclusions, which, even if they did not always come into line with results of observation and experiment, we should be compelled to prefer. It is only from his more elevated position that a general can follow the course of a battle; whilst the private with his experience confined to a limited area of the field of conflict may form the most erroneous ideas of the progress of the fight. So it is with observers whose employment it is to struggle with the details and secondary principles of plant-distribution, and so it is with the generaliser who has already roughly mapped out the principal features of the main problem.

When Mr. Bentham in 1869, remarking on the paucity of species common to tropical Asia and America, characterised them either as plants wholly or partially maritime and spread by the currents, or as weeds dispersed by cultivation over the warm regions of the globe, he mentioned amongst the plants in the former category, Gyrocarpus jacquini. This tree presents one of the mysteries connected with the Pacific islands; and I don't imagine that this eminent botanist could have known anything except inferentially as regards the mode of dispersal of its fruits. Yet experiment shows how well founded the inference was, whilst behind it lay a life-time of botanical research.

The author thus approaches the subject of the floras of the Pacific islands rather as a plotter of detail than as a delineator of great designs. However much we may study the means of dispersal, we have behind them the great facts of distribution, serving like the main stations of a trigonometrical survey, and with these we have to make our lesser facts and observations square. One is conscious all the time that much of what seems new in one's researches has already been foreseen by the generaliser, and that one can do little else than assist in confirming some of his results. This is all that I can lay claim to in this work.

The floras of the islands and coasts of the tropical Pacific are here regarded entirely from the standpoint of plant-dispersal. The fruits and seeds rather than the flowers have been the subject of my investigations; and although there is much to please the eye

in the flora of a Pacific island, it was always with a sense of disappointment that I turned away from some pretty flowering plant that failed to present me with its seed. Amongst the wonders of the plant-world rank the Tree Lobelias of the Hawaiian Islands; yet their greatest charm to me lay not so much in their giant-flowers and their arborescent habit as in the mystery surrounding the home of their birth and their mode of arrival in these islands. When I first stood under the shade of the lofty Dammara vitiensis, the Kauri Pine of Fiji, all my interest lay in its cones lying on the ground; and I remember how eagerly I handled my first specimen, and how anxiously I watched its behaviour when experimenting on its capacity for different modes of transport. When a strange plant presented itself on a beach, my first care was to ascertain the fitness of its fruits or seeds for transport by the currents; and all inland plants with fruits likely to attract frugivorous birds were at once invested with a special interest for me.

The mangrove swamps were always great places of interest, and months of my sojourn in the Pacific must have been passed in exploring their creeks and in examining their vegetation. Botanists usually avoid these regions; but the observation of the germination of the Rhizophora fruits on the trees and the inquiries connected with their methods of distribution over the oceans were pursuits so engrossing that I ignored the numerous discomforts connected with the exploration of these gloomy regions. The magnificent mangrove forests of the Ecuador coast of the Pacific will live longest in my memory, though the risks were considerably greater and the discomfort of existence extreme. But the mangrove swamps present us with glimpses into the conditions of plant life during the warmer epochs of the earth's history, when perhaps the seed-stage was largely dispensed with, whilst an atmosphere, laden with moisture and screening off much of the sun's light, enveloped most of the circumference of the globe.

The plant world viewed only from the standpoint of dispersal may lack much that is pleasing to the eye, though it abounds with small and great problems fascinating to the reason. Matters of great moment are here involved, and in the case of the Pacific islands they concern not only the source of the oceanic floras, but the story of the islands themselves; whilst behind these there rise up questions of yet deeper import, questions that are bound up with the beginnings of genera and species, and with other mysteries of life on the earth. The distribution of plants presents something

more than a problem of means of dispersal, or a problem of station, or a problem of plant migration connected with climatic changes. It is something a great deal more than all three, since it is indissolubly connected with a past, of which unfortunately we know very little. Let us take it to be a question of means of dispersal, and then in imagination transporting ourselves to the Scandinavian coast, let us gather up the stranded West Indian beans of Cæsalpinia, Mucuna, and Entada, that have been drifted there for ages by the Gulf Stream, and lie in some cases semifossilised in the adjacent peat-bog. Was ever dispersal so utterly purposeless as this? Yet here lies a principle of plant-dispersal that is fundamental. We see it in the thistle-seed floating seaward in the wind. Nature never intended its pappus for such an end. It was formed for quite another purpose, yet it aids largely the dispersion of the plant. What can be more significant than that?

Or let us take it to be a matter of station. Given time and the recurrence of the same conditions, with others I once imagined that we could explain most things in plant-distribution, whether of plants at the coast or of plants inland, whether of plants of the alpine peaks or of plants of the plains, or of plants of the river or of the pond. Time, it was held, had long since discounted the means of dispersal, and distribution became merely an affair of station. But the supplanting of many indigenous species of a flora by introduced species is a common story in the plant-world; and such a view needs no further discussion here. Nor is distribution only concerned with plant-migration. Any theory of the origin of alpine floras on tropical mountains will have to explain the presence of the temperate genera, Geranium and Sanicula, not alone on the summits of the mountains of Equatorial Africa and Madagascar, but on the uplands of Hawaii in mid-Pacific, where also are found Ranunculus, Vaccinium, Fragaria chilensis (the Chilian strawberry), and Drosera longifolia.

Taking genera of different stations each in their turn, and following up the clues thus afforded, it would be possible to find support for all the reputable views relating to plant-distribution. The wide range of aquatic plants under conditions that completely change the character of the terrestrial vegetation, such, for instance, as Myriophyllum and Ceratophyllum, might be plausibly attributed to the relative uniformity of the conditions of aquatic life both in time as well as space. The occurrence of Vaccinium on mountain-tops over most of the world, even on the highlands

of Samoa, Tahiti, and Hawaii in the Pacific Ocean, would be rightly regarded as evidence of active dispersal of the seeds through the agency of birds from one mountain-summit to another, whether in mid-ocean or in the centre of a continent. The prevalence of the same beach-plants over most of the globe in the same climatic zones would point unmistakably to the predominant agency of currents. But with many plant-genera, some of which range the world, whilst others again may be restricted to a single group of islands in the Pacific, there is often no question either of means of dispersal, or of station, or of plant-migration, and problems of a very different nature are opened up.

When we leave the beach and the mountain-top, the river and the pond, all the troubles of distribution begin; and since but a small proportion of plants in a typical flora belong to these stations, it follows that difficulties will dog our steps with the large majority of the plants. The agencies of dispersal now working around us, the current, the wind, the insect, the bird, and the bat, will explain many of the features of littoral and alpine floras and of the vegetation of ponds and rivers. Here we have in so many cases wide-ranging genera with the means of dispersal ready to hand. We can connect the wide range of Vaccinium with the wide range of birds of the grouse and other families that feed on the berries. We can associate the great areas of aquatic or sub-aquatic genera, like Potamogeton and Sparganium, with the migratory habits of the ducks in the stomachs of which we find their seeds. We can connect the great ranges of beach plants like Ipomea pes capræ in the tropics, and Convolvulus soldanella in the temperate regions with the currents, and the almost cosmopolitan range of many ferns and lycopods with the winds and other agencies.

When, however, we enter the forests we find genera that are often much more restricted in their areas, and species that are yet more limited in their range. There is very little dispersal going on here. The birds are strange. Their distribution is usually very local. They look lazily down at us from the branches, as they disgorge the seeds and stones of the fruits they have eaten, which cover the ground around. We can almost fancy that they say:—"Our work is done. We rest from the toil of our ancestors. They carried seeds to far-distant Hawaii, Tahiti, and Savaii. Our work is done." And as we walk through those noiseless forests, where the machinery of species-making is ever in silent motion, we become aware that we are treading one of Nature's great work-shops for the manufacture of species and genera. Outside the

forest all is bustle and hurry. We are in the streets, or rather in the distributing areas of the plant-world. We hear the noise of the breaker, the roar of the gale, the cry of the sea-gull, the flapping of a myriad pairs of wings of some migrating host overhead, and we know that the current, the wind, and the bird are actively at work; but their operations are confined mainly to the beach, the mountain-top, the river, and the pond.

Let us take a well-wooded Pacific island several thousand feet in height. We find on its beaches the same littoral plants that we have seen before on the tropical shores of Malaya, of Asia, of Africa, and of America. We find in its ponds and rivers the same species of water-plants, such as Ceratophyllum demersum, Ruppia maritima, and Naias marina, that are familiar to us in the cool and tepid waters of much of the globe. On its level summit, if it remains within the clouds we find in the boggy ground, where Sphagnum thrives, genera that are represented in Fuegia, New Zealand, and the Antarctic islands, such as Acæna, Lagenophora, and Astelia, and the world-ranging Drosera longifolia. In other elevated localities we find Ranunculus, Geranium, Sanicula, Artemisia, Vaccinium, and Plantago, chiefly genera of the temperate regions of the northern hemisphere; whilst there are also found Gunnera, Nertera, and Uncinia, all hailing from the south and belonging to the Antarctic flora characterising all the land-area around the globe in the latitude of New Zealand and Fuegia. The Hawaiian species of Nertera and of Uncinia occur also in New Zealand, and the first-named is found also in Tristan da Cunha and in South America. In the Hawaiian uplands there is also to be seen Deyeuxia, a genus of grasses found in the Tibetan highlands and in the Bolivian Andes at elevations of 16,000 to 19,000 feet; and the same species that exists in Australia may be found in the mountains of Hawaii. Here also, both in Hawaii and Tahiti, occurs Luzula campestris.

In making the foregoing remarks on the alpine plants of a Pacific island, I have had Hawaii in my mind, but we find the elements of a similar widely-distributed mountain-flora in the less lofty peaks of Tahiti and Samoa, and traces even in Fiji, where the mountains, however, have only a moderate elevation. But the point I wish to lay stress on is the cosmopolitan yet temperate character of the mountain-flora of an island lying in the midst of the tropical Pacific. As he shifts his station on this mountain-summit, the observer might at different times imagine himself in the Sierra Nevada of California, on a Mexican tableland, on a peak

of the Andes, or in the lowlands of Fuegia. Other plants that I have not mentioned, such as Coprosma, would bring back to him New Zealand. He might even be on a mountain-top in Central Africa, or on a Madagascar plateau ; whilst in the boggy region of an elevated Hawaiian tableland he would meet with not only the physical conditions, but also several of the plants found on the higher levels of Tristan da Cunha.

It is, however, to be noted that although these mountain-tops in the mid-Pacific have been stocked with genera from the four quarters of the compass, the species as a rule are restricted to that particular archipelago. Whilst the beach and the river in most cases possess plants that have very wide ranges over the earth, a good proportion of the species on the mountain-summit are not found elsewhere. This implies a partial suspension of the means of dispersal on the mountain-top, whilst the currents and waterfowl are still actively distributing the seeds of the littoral tree and of the aquatic plant. We here get a foreshadowing of another great principle, or of another line along which Nature has worked in stocking these islands of the Pacific with their plants, a subject concerning which much will be said in later pages.

Hitherto, we have dealt only with a small proportion of the flora, and with but a small portion of the area of the island. We have yet to deal with the intermediate region between the sea-border and the summit of the island, or, in other words, with the forested mountain slopes. This is the home of many of the peculiar species and peculiar genera, both of plants and birds ; and it is with this zone that we shall be mainly concerned when we come to contrast the floras of the several archipelagoes of the tropical Pacific. Here the agencies of dispersal have, to a large extent, ceased to act ; and the question will arise as to the connection between the endemic character of the plants and the endemic character of the birds. We shall have to ask why this island, after receiving so many plants, ceased to be centres of dispersal to other regions. It is possible that these seeds or fruits have lost their capacity for dispersal ; but only a few instances of this change present themselves. Rather it may be supposed that the birds that originally brought the seeds to the island came to stay ; and this at once suggests another query as to the cause of the change of habit. I am alluding here not to the plants with minute seeds, such as Sagina and Orchis, which Mr. Wallace, in his *Darwinism*, regards as capable of being transported by strong winds over a thousand miles of sea ; but to those numerous plants found in

the Fijian, Tahitian, and Hawaiian forests, where the seeds and "stones" are large and heavy, measuring often as much as a quarter of an inch (6 mm.), and sometimes nearly an inch (25 mm.) in size. The reader will be surprised to learn how little "size" has determined the distribution of seeds and fruits in the Pacific. He will have to appeal to the habits of pebble-swallowing of the Dodo, the Solitaire, the Goura pigeon, the Nicobar pigeon, &c., if he desires to find a parallel in the habits of birds.

It is here assumed that the reader is already acquainted with the principles involved in a discussion of island-floras, principles clearly laid down in the writings of Hooker, Wallace, Hemsley, and others. As a general rule in an island or in a group of islands where there are a large number of plants not found elsewhere, there is also a large endemic element in the avifauna, and where none of the plants are peculiar, endemic birds are either few or wanting. As an example of the first we may mention Hawaii, and Iceland affords an instance of the second. But there is no hard and fast rule connecting the endemic character of the plants and birds of an island with its distance from other regions. Even the small group of Fernando Noronha, lying only some 200 miles off the coast of Brazil, possesses its peculiar birds and its peculiar plants; and we can there witness the singular spectacle, as described by Mr. Ridley, of an endemic bird, a frugivorous dove, engaged in scattering the seeds of endemic plants over the little group. This is the only fruit-eating bird in the islands, remarks the same botanist in the *Journal of the Linnean Society* (vol. 27, 1891); and "when one sees the number of endemic species with edible fruits, one is tempted to wonder if it were possible that they were all introduced by this single species of dove, or whether other frugivorous birds may not at times have wandered to these shores." This inter-island dispersal in a particular group of peculiar plants by peculiar birds is a common spectacle in the Pacific. The contrast between the large number of plant-genera possessing fruits that would be dispersed by frugivorous birds and the poverty of fruit-eating birds in the avifauna is well displayed in Hawaii.

The island of St. Helena would seem to offer an exception to the rule that endemic birds and endemic plants go together, since, though its flora possesses a very large endemic element, there are scarcely any endemic or even indigenous birds recorded from the island. We can never know, however, how much of the original fauna disappeared with the destruction of the forests. It would nevertheless appear that but few of the genera possessing

peculiar species of plants were adapted for dispersal by frugivorous birds. The lesson to be learned from this island concerns the Compositæ, often arboreous, that constitute the principal feature of its flora. St. Helena retains almost more than any other island evidence of the age of Compositæ which has left its impress on many insular floras; and when we discuss the original modes of dispersal of the endemic Hawaiian genera of the same order we shall look to the flora of this Atlantic island for assistance in the matter. To the age of Compositæ belong the beginnings of several insular floras.

To return to the main line of our argument, it would seem that in a Pacific island there is a constant relation between free means of dispersal and the preservation of specific characters. The ocean-current and the aquatic bird are in our own time actively engaged in dispersing the seeds of shore-plants and water-plants, and we see the same species ranging over the world. On the other hand on the mountain-top the agencies of dispersal are beginning to fail, and as a result many a mountain has some of its species restricted to its higher regions. In the forest zone there has been a more or less complete suspension of the activity of the dispersing agencies, and new genera are formed whilst peculiar species abound. Free means of communication with other regions restrains but does not arrest the differentiating process that is ever in progress throughout the organic world. Isolation within certain limits gives it play.

It is in this connection interesting to reflect that during the differentiation of the inland flora the littoral plants have lagged behind or have remained relatively unchanged. The currents have been working without a break throughout the ages; and the cosmopolitan Ipomea, that now creeps over the sand of the beach, or the wide-ranging Rhizophora, that forms the mangroves of the coast-swamp, must have witnessed the arrival of the ancestors of several of the endemic inland genera. The swamp-plants of the littoral flora are probably older, however, than the beach-plants which have been recruited from time to time in one region or another of the tropics from the inland flora. Yet as a body the littoral plants have lagged far behind the inland flora. We might thus expect that in a Pacific island, excluding the wind-distributed plants, such as the ferns and the lycopods, the most ancient types of the plants would be found at the coast, the most modern in the forests, whilst the plants of the mountain-summit would represent an intermediate age.

But true as this may be, the composition of a strand-flora is a very complex one. Although, as Prof. Schimper remarks, the mangrove formation is more isolated than the beach formation, and affords evidence of a much earlier separation, the beach-plants as a body are anything but homogeneous in their character. Their physiognomy varies to some extent with the alteration in the characters of the inland flora, changes to which the mangrove formation makes a very slow response. Yet amongst the plants of the beach we find strangely assorted forms that are as ancient denizens of the coast as the mangroves themselves. Take, for instance, Salsola Kali, that thrives alike on a beach in Chile, on the sea-shore in Devonshire, and in the salt-marshes of the interior of Tibet. Then, again, there is a type of littoral plant, of which Armeria vulgaris and Plantago maritima may be taken as examples, which is equally at home on the beach and on the tops of inland mountains. We might in a sense apply the wrecker's motto,

"What the sea sends and the land lends,"

to the history of a littoral flora. Yet on the other hand the inland flora in its turn receives a few recruits from the littoral flora; and it is the relation between the inland and coast species of the same genus that offers one of the most fascinating studies in the botany of the Pacific Islands.

This introductory chapter may be concluded with a few remarks on what may be termed "the ethics of plant-dispersal." Not that this is in any way a suitable phrase, but it best expresses my sense of the lack of propriety in some things connected with this subject. It is odd, for instance, that we speak of the dispersal of plants and animals in the same breath, as if the process was in both cases identical. Seeing that from this point of view we judge a plant only by its seeds and fruits, it is apparent that we are following quite a different method than that which we employ in the study of the dispersal of animals. Whilst the zoologist classifies the units of dispersal, the botanist does nothing of the kind; and the two systems of classification are at the outset fundamentally distinct. The student of plant-dispersal thus often finds himself placed in an awkward dilemma. For him a family is a collection of allied genera having similar seeds or fruits and fitted often for the same mode of dispersal. A family like Sterculiaceæ, possessing such a variety of seeds and fruits suitable for very different modes of dispersal, is from his standpoint a collection of dissimilar units. Genera like Commersonia,

Waltheria, Kleinhovia, Sterculia, and Heritiera, that he so often meets with in the Pacific Islands, have in these respects frequently very little in common; and yet one of the earliest determining influences in plant-life must have lain in the capacity for dispersal.

Yet chance seems to reign in the processes of plant-dispersal ever going on around us. In the floating seed, in the achene with its light pappus blown before the gale, in the prickly mericarp entangled in the plumage of a bird, in the "stone" of the drupe disgorged or ejected by the pigeon, in the small grain that becomes adhesive in the rain, in the tiny rush-seed enclosed in the dried pond-mud on the legs of some migratory bird, in all these we see the agencies of dispersal making use of qualities and of structures that were developed in quite another connection and for quite another purpose. That such characters have been so to speak appropriated by these agencies is a pure accident in a plant's life-history. If the evolutionary force had been in operation here, it would have selected some common ground to work on. There would have been some uniformity in its methods, whereas the modes of dispersal are infinite. The qualities and characters that happen to be connected with dispersal belong to a plant's development in a particular environment. They can never have been adapted to another set of conditions that lie quite outside that environment. There is a relation of a kind between the specific weight of wood and the density of water, and this, in a sense, sums up the connection between a seed and its distributing agencies.

Evolution has never concerned itself directly with means of dispersal. Evolution and Adaptation represent the dual forces that rule the organic world, the first an intruding force, the last a passive power representing the laws governing the inorganic world. To these laws the intruding power has often been compelled to bend, and it has had to pay its price, and sometimes it has succumbed, and sometimes it has turned its defeat into a victory. Nature, so watchful over the young plant, as represented by the seed, is finally compelled to let it go, and dispersal begins where evolution ends, or rather when the evolutionary power fails. The seed-stage itself is the price of adaptation. The death of the individual may also be regarded from the same standpoint. It represents a defeat of the evolutionary force, which, however, has been retrieved by the gift of reproductive power.

CHAPTER II

THE FLORAS OF THE PACIFIC ISLANDS FROM THE STANDPOINT OF DISPERSAL BY CURRENTS

The initial experiment.—The proportion of littoral plants.—The two great principles of buoyancy.—The investigations of Professor Schimper.—The investigations of the author.—The great sorting process of the ages.—Preliminary results of the inquiry into the buoyancy of seeds and fruits.

IN the previous introductory chapter some of the numerous questions affecting insular floras were briefly referred to. I will now ask my reader, if he has had the patience to read it, to consign that chapter for the time at least into oblivion, and to proceed with me to our Pacific island with the intention of investigating its flora from the standpoint of dispersal. We will together take up the subject *de novo*, after banishing from our minds all preconceptions that we may have possessed.

After having been over the island gathering specimens of all the seeds and fruits, we return to our abode on the beach. But we are puzzled where to begin. The problem presents itself as a tangled skein, and our difficulty is to find an "end" that we can follow along with some chances of success. In our trouble we look around us; and at that moment we see a number of floating seeds and fruits carried by the current past the beach. This presents us with a clue and our investigation begins.

We place all our seeds and fruits in a bucket of sea-water and notice that many of them sink at once. In a few days we look again and observe that many more are at the bottom of the bucket, only a small percentage remaining afloat. We then remark to our surprise that nearly all of the floating seeds and fruits belong to coast plants, those of the inland plants, which indeed make up the great bulk of the flora, having, as a rule, little or no buoyancy. After a lapse of weeks and months the seeds and fruits of the


OCEANIA
English Miles
0 200 400 600 800 1000
One Hundred Fathoms Line shown thus
PACIFIC
Micronesia
Melanesia
Polynesia
Hawaii or Sandwich Islands
Marianne or Ladrones (German)
Caroline Islands (German)
Marshall Archip.
Gilbert Is. (Brit)
Central Polynesian Sporades
Phoenix Is.
Lagunes or Ellice Is. (Brit)
Tokelau or Union Is. (British)
Manahiki Islands (Brit)
Marquesas or Mendaña Islands (French)
Society Is. (French)
Paumotu or Low Archipelago (French)
Samoa or Navigator Is.
Tonga or Friendly Is. (Kingdom)
FIJI Is. (British)
Hervey or Cook Is. (British)
Austral or Tubuai Is. (French)
New Hebrides
Loyalty Is.
New Caledonia
Solomon Is.
Bismarck Archip.
NEW GUINEA
Kaiser Wilhelms Ld.
QUEENSLAND
CORAL SEA
Tropic of Cancer
Equator
Tropic of Capricorn
Long. East 170 of Greenw.
Long. West 170 of Greenw.
John Bartholomew & Co., Edin.

coast plants are found to be still afloat. In the results of this experiment we see the work of the ages. There has been, in fact, a great sorting process, during which Nature has "located" the plants with buoyant seeds or seed-vessels at the sea-coast, placing the others inland. This is the clue that we shall follow up during many chapters of this book; and having in this manner introduced the reader to the subject, I will now refer to the general results of my investigations in this direction in the Pacific Islands.

In Fiji there are about eighty littoral plants out of a total of at least 900 species of indigenous flowering plants, that is to say about nine or ten per cent. (Note 1), the littoral grasses and the sedges being with one or two exceptions excluded. These shore plants belong to the sandy beach and to the coast swamp, and most of them are distributed over the tropical shores of the Indian and Pacific Oceans, whilst not a few occur on the coasts of tropical America. They form the characteristic plants of the coral atoll, and many of them have long been known to be dispersed by the currents. From the list given in Note 2 it will be seen that these eighty species belong to about seventy genera. Nearly all of them (95 per cent.) possess seeds or seed-vessels that float at first in sea-water; whilst three-fourths of them (75 per cent.) will float unharmed for two months and usually much more, and several of them will be found afloat after a year or more, being still capable of reproducing the plant (Note 3).

The prevalence in the Fijian strand-flora of Leguminosæ, which are included in my list under the divisions Papilionaceæ, Cæsalpinieæ, and Mimoseæ, is very significant. They make up about 29 per cent. of the total. Excluding weeds and a few other introduced plants, there are some fifty species known from the Fijian Islands, and of these almost half belong to the littoral flora, which as we have seen constitutes only a fraction (one-tenth) of the whole flora. If we regard the genera, we find that out of some thirty Leguminous genera twenty are littoral and in most cases exclusively so. This conspicuous feature in the constitution of the strand-flora is of prime importance as concerns the question of adaptation to dispersal by currents, since nearly all the Leguminosæ with buoyant seeds offer themselves as defiant exceptions to any such law.

I will now contrast the Fijian inland flora with that of the coast from the point of view of the buoyancy of the seed or fruit, according as it presented itself for possible dispersal by currents. Rather over a hundred plants were experimented upon (Note 4).

After excluding some introduced plants there remain some ninety species belonging to about sixty genera, and of these quite 75 per cent. sank at once or in a few days. I may add that all kinds of fruits are here represented, the capsule, the achene, the coccus, the berry, the drupe, &c. Of the buoyant residue few possess seeds or fruits that will float uninjured for any length of time. Not many gave indications directly in opposition to the principle that whilst the seeds or fruits of shore-plants generally float, those of inland plants usually sink, since as pointed out in Note 5 most of the difficulties are removed during the subsequent developments of the principle discussed in the later pages of this work or are to be explained on other grounds stated in the note.

We pass now from Fiji as typical in its flora of the Western Pacific to Tahiti as representing in its flora the more strictly oceanic groups of Eastern Polynesia. In the Tahitian region, which is taken as including in a general sense the Society Islands, the Marquesas, and the Paumotus, there are only between 50 and 60 littoral plants, excluding the occasional additions from the inland flora. As indicated by the letter T preceding the species in the list of Fijian shore plants, nearly all are to be found in Fiji, and the few not yet recorded from that group, which I have referred to in the remarks following the list, will probably be found there by some subsequent investigator. In Tahiti also between 75 and 80 per cent. of the strand plants have seeds or seed-vessels that float for months; and here also Leguminosæ predominate, forming about 30 per cent. of the total. A conspicuous negative feature in the Tahitian strand-flora is concerned with the absence of the mangroves and their numerous associated plants, which together form the mangrove formation in Fiji. This remarkable character in the distribution of shore plants in the Pacific is discussed in Chapter VI.

Not having visited Tahiti, I can only deal inferentially with the inland plants, as in the case of the strand-flora. Here also the plants are in the mass Fijian in a generic and often in a specific sense, and there is no reason to believe that the principle involving the non-buoyancy of the seeds or fruits of inland plants does not as a rule apply to Tahiti as well as to Fiji.

The Hawaiian Islands, standing alone in the North Pacific, form a floral region in themselves, a region that is the equivalent not of one group in the South Pacific, such as that of Fiji or of Tahiti, but of the whole area comprising all the groups extending from Fiji to the Paumotu Archipelago. Lying as it does mainly

outside the zone of influence of the regular currents that would bring the seeds of tropical plants to its shores, Hawaii possesses a strand-flora that is meagre in the extreme. Not only does it lack the mangrove formation so characteristic of Fiji, but it lacks also many of the plants of the beach formation that are found both in Fiji and in Tahiti, plants that give a peculiar beauty to the reef-girt beaches all over the South Pacific. Its poverty is sufficiently indicated in the number of its species, thirty in all, barely more than half of the number found in Tahiti, and not much over a third of those occurring in Fiji. Though coral reefs with their accompanying beaches of calcareous sand are relatively scanty, the characteristic littoral plants have not been numerous enough to hold their own against intruders from the inland flora, and endemic species have taken a permanent place amongst the strand plants. The Hawaiian strand-flora has thus quite a facies of its own, and it will be found discussed in Chapter VII., whilst a list of the plants is given in Note 28. It will thus not be a matter for surprise that the littoral flora of Hawaii follows the principle of buoyancy only in a modified degree. It is true that about two-thirds of the species of the present beach flora possess seeds or seed-vessels that float for months; but since there are reasons for believing that several of them are of aboriginal introduction, this proportion is reduced to a third. In the list of the Fijian shore plants given in Note 2, those occurring also in Hawaii are preceded by H.

When we look to the Hawaiian inland flora for indications respecting the principle of the non-buoyancy of the seeds or seed-vessels of inland plants, we find that so far as it has been there tested this principle receives fresh support from the plants growing on the slopes of the Hawaiian mountains. Although the author was only able to sample the inland flora, we have in the list given in Note 6 all kinds of plants, from the forest-tree to the herb, and most varieties of fruits. Excluding a few introduced plants, there are in this list about fifty species of indigenous plants belonging to about forty genera. Of these plants quite 80 per cent. possess seeds or fruits that sink either at once or in a week or two. Of the "buoyant" residue very few have seeds or fruits that will float for months. These apparent exceptions to the principle are in great part capable of being explained on the grounds referred to in Note 5 in connection with the Fijian inland plants; and I have alluded to them in Note 7.

The littoral flora of Fiji is essentially Malayan and Asiatic, and for our purpose is eminently typical. Its plants are found far and

wide on the tropical coasts of the Old World, and sometimes also in the New World. In more than half the species we are concerned with the dispersal by currents of more or less dry indehiscent fruits that range usually in size from a marble to a cricket-ball, as illustrated by those of Hernandia peltata and Barringtonia speciosa, whilst with most of the rest the currents distribute large seeds, several of which are Leguminous, as in the case of Mucuna, Cæsalpinia, and Entada, with others of the Convolvulus type, as in the instance of Ipomea pes capræ. It is remarkable that in selecting plants with buoyant seeds or seed-vessels for a station at the coast Nature has generally ignored those with very small seeds. When such small seeded plants, as Sesuvium portulacastrum, occur on the beach, the seeds have as a rule no buoyancy. Pemphis acidula is, however, an exception; but its case is a very rare one. It will be established in the next chapter that the non-buoyancy of small seeds is generally true also of plants growing by the river or by the pond.

The point at which we have arrived in our inquiry concerning the general collection of seeds and seed-vessels that we placed in sea-water is that *the plants with buoyant seeds or seed-vessels have been for the most part "located" at the coast.* But if we look a little more closely at the sunken and floating seeds, we find that in the same genus there are species with seeds or seed-vessels that sink and species with those that float. We look again and then perceive that the same general principle is true of different species of the same genus growing inland and at the coast. We learn now that as a rule when a genus possesses both littoral and inland species, the seeds or fruits of the former float in sea-water for a long time, whilst those of the latter have little or no floating power. But we have yet to examine the structure of the coverings of the buoyant seed or fruit; and we shall then discover that the different behaviour in water is often associated with corresponding structural differences of a striking character. The structural causes of buoyancy are dealt with in Chapter XII.; and we will now content ourselves with enunciating the second principle that *in a genus comprising both coast and inland species, only the coast species possess buoyant seeds or seed-vessels.*

The important principle above indicated was not altogether new to me, as is shown in the next chapter. But it was new in the case of the floras of the Pacific Islands. When it first presented itself in Hawaii I was engaged in trying to find a connection between the inland and littoral species of Scævola; and its discovery led me

to form a plan worthy almost of Don Quixote, namely, to cultivate the beach species of Ipomea, Scævola, and Vitex in the interior with the hope of finding them converted into inland species when I returned to Hawaii after a lapse of years. Little matters often determine a career, and for a while my future movements and probably the remainder of my life were largely centred around my interests in the well-being of Scævola Kœnigii. The scheme was actually undertaken, and I had fixed on a little plot of land at the foot of the mountains rising behind Punaluu in Kau. The transaction was on the point of completion when the owner changed his mind and the plan fell through. Subsequent observation and reflection have led me to believe that in most cases no connection exists between the littoral and inland species of a genus ; and I have dwelt on this incident merely to show the importance that I rightly attached to this distinction, whilst misinterpreting its meaning.

But to return to my own investigations. Had I indeed read more carefully Professor Schimper's work on the Malayan strand-flora, this subject would have been found discussed by an observer far abler than myself, though from a very different standpoint, that of Adaptation and Natural Selection. He points out (pp. 179—182) that with a number of these tropical genera possessing both littoral and inland species, such as Barringtonia, Calophyllum, Clerodendron, Cordia, Guettarda, and Terminalia, greater buoyancy of the fruits of the shore species is associated with certain structural characters in the fruit-coverings, whilst with the inland species, where the floating power of the fruits is either much diminished or entirely absent, these structural characters are either less developed or lacking altogether.

The question of structure and the debateable matters concerned with it are treated at some length in Chapters XII. and XIII., and Professor Schimper's views are there given. I will content myself with remarking that the genus Terminalia was especially studied by him in this respect. He tested the buoyancy of the fruits of ten species, and found that the flotation period varied from nothing to 126 days and more. By far the best "floaters" were the fruits of Terminalia Katappa, the only littoral species tested, all the others being inland species with less buoyant fruits, and diminished ranges, some of the fruits sinking at once, whilst the others sank usually in a few days or in a few weeks. It was also ascertained that, although the buoyant tissue in the fruit-coats varied in amount generally with the floating-powers,

it was rarely absent altogether in the inland species, a very significant conclusion, as will subsequently be pointed out.

Several other striking examples of this principle came under my notice in the Pacific, and perhaps the most significant is that of Scævola, a genus of the Goodeniaceæ, confined mainly to Australia and the Pacific islands, but possessing also a littoral species, S. Kœnigii, that is found on tropical beaches all round the globe. It is associated in both Hawaii and Fiji with inland species, none of which are common to the two archipelagoes, and in the case of the Hawaiian species not found outside the group. All the species have fleshy drupes, both coast and inland plants, the "stone" in the littoral species possessing a thick covering of buoyant tissue, which is absent or but slightly developed in the inland species. The fruits of the shore species float for many months; whilst those of the inland species experimented on by me (S. Chamissoniana and S. Gaudichaudii in Hawaii, and S. floribunda in Fiji) sank at once or within a few hours. Here we are only concerned with the difference of buoyancy between inland and littoral species. The several other questions involved concerning this genus will be dealt with later on in this work.

The genus Morinda offers another good example of this principle. It includes one widely-spread littoral species (M. citrifolia), found not only in all the Pacific archipelagoes, but also over much of the tropics. It is associated in all the large groups with one or more inland species, some of which are endemic and others more generally distributed. The littoral species displays in its pyrenes a singular air-cavity, the nature of which is discussed in Chapter XII., which endows them with great floating powers. This cavity is not found in inland species, and the pyrenes have in consequence no floating power (see Note 8).

Calophyllum Inophyllum, an Old-World littoral tree, spread far and wide over the Pacific islands, has very buoyant fruits. In the groups of the South Pacific it is associated with inland species that are commonly found in the forests, namely, C. spectabile and C. Burmanni, the fruits of both of which, according to my observations in Fiji, have limited floating powers, sinking after periods varying from a few days to four weeks, and lacking in great part the buoyant coverings of the littoral species. Professor Schimper obtained similar results with inland species from other regions (Note 9).

The fruits of the two Fijian coast trees, Barringtonia speciosa and B. racemosa, possess great floating powers; whilst those of an

undescribed species that I found in the mountains of Vanua Levu sink at once. Another Fijian inland species (B. edulis, Seem.) that is often planted, has fruits that float heavily for about a month. This difference in buoyant powers is also associated with characteristic differences in the structure of the fruits. It would be interesting to learn what floating capacity belongs to those of the Samoan endemic species (B. samoensis, Gray). Professor Schimper's observations on the genus in the Malayan region point in the same direction, but more than one difficulty awaits its solution in the re-examination of the genus. He says, however, that B. excelsa, Bl., a Malayan species, sometimes cultivated and growing both inland and at the coast, has fruits that floated for one hundred days after drying (p. 173).

A striking instance of this principle is afforded in the case of the two Fijian species of Tacca, the wide-ranging littoral species, T. pinnatifida, where the seeds float for several months, and the inland species, T. maculata, Seem., found also in Australia and Samoa, where the seeds sink at once or in a few days. The seeds of the shore plant owe their buoyancy to the spongy tissue in their coverings, which is either absent or much less developed in those of the inland species. This point might also be determined for the new Samoan inland species described by Reinecke, the German botanist, as T. samoensis.

Another good illustration is afforded by the two species of Premna of the South Pacific, though here the buoyancy of the "stone" of a drupe is concerned. With P. taitensis or P. integrifolia, a small littoral tree or shrub, these stones possess great floating-power, and are often found in the floating seed-drift of the Fijian estuaries and in the stranded drift of the beaches. In the case of Premna serratifolia, an inland tree of moderate size, the stones have as a rule little or no buoyancy. As shown in Note 32, where this genus is discussed in detail, the buoyancy is mainly due to empty seed-cavities.

Other instances might be given in illustration of this principle; but it will have been noticed that already many of the familiar trees and shrubs of a tropical beach have been mentioned in this connection either by Professor Schimper or by myself. There are other genera that afford similar indications but in a less direct fashion.

For instance, there are three widely spread Leguminous beach plants of the Pacific, Erythrina indica, Canavalia obtusifolia, and Sophora tomentosa, none of which are found in Hawaii; but

in that group the genus is represented in each case by an inland species, Erythrina monosperma, Canavalia galeata, and Sophora chrysophylla, the last two species being peculiar to those islands. The seeds of the three littoral species will float for a long time in sea-water, whilst those of the three Hawaiian inland species have no buoyancy. I may say that some very interesting questions relating to the origin of these inland species are here raised. They will be discussed in a later chapter (Chap. XV.).

There are a number of plants belonging to the Convolvulaceæ in these islands that behave in an irregular way in flotation experiments; but their inconstant behaviour can in most cases be explained in accordance with the principle that in the same genus the shore species have buoyant seeds and the inland species non-buoyant seeds. Thus, whilst the seeds of the littoral species, Ipomea pes capræ, I. grandiflora (Lam.), and I. glaberrima (Boj.), can float for long periods, and those of the inland species, I. pentaphylla, I. tuberculata, and I. Batatas (Sweet Potato), have no buoyancy, the seeds of other inland species, I. insularis (Steud.), I. bona nox (L.), and I. turpethum (R. Br.), are inconstant in their behaviour. The three last-named species are, however, to be found also flourishing at times at and near the coast, and the varying floating powers of their seeds may probably be connected with their varying stations. This is indeed suggested by the case of Argyreia tiliæfolia in Hawaii, in which in my experiments the seeds of plants growing at the coast floated, sometimes for months, whilst those from inland plants sank.

This behaviour of the Convolvulaceæ becomes yet more intelligible, and more in accordance with the principle, when we reflect that the cause of buoyancy is not concerned with the seed-coats or with the nucleus, neither of which are able to float, but with the air-spaces left by the incomplete filling-up of the seed-cavity by the crumpled embryo. The extent to which the seed-cavity is filled up varies not only between different genera and between different species of the same genus, but also amongst individuals of the same species. Even the seeds of Ipomea pes capræ, amongst the most typical of floating seeds, display this variation, and they show it also in their floating power, since about a third of the seeds usually sink during the first month or two of the flotation experiments. We can thus explain also why in the case of Ipomea insularis seeds from Fiji floated for months, whilst those from Hawaii had no floating power.

The seeds of the different species of Hibiscus also appear to

behave very irregularly; but even here most of the difficulties can be removed, when we come to consider a further extension of the principle. Thus, whilst the seeds of Hibiscus tiliaceus, a wide-ranging littoral tree known to be dispersed by the currents, float for a long time, those of H. Youngianus (Gaud.), an endemic Hawaiian species, and of two wide-ranging species, H. diversifolius (Jacq.) and H. Abelmoschus (L.), also float for some time. The Hawaiian plant, however, grows in wet places; and this applies also to H. diversifolius which grows in swamps at and near the coast. The extension of the principle to water-side plants generally, which is discussed in the next chapter, will explain the difficulties connected with these two species. But we have in H. Abelmoschus a remarkable exception to any rule of buoyancy, since it grows in dry situations, is often cultivated, and yet possesses a special layer of buoyant tissue in the seed-coats to which the floating power is due. The seeds of Hibiscus esculentus (L.), the widely spread cultivated plant of the tropics, have no buoyancy.

Some curious indications are supplied by Cæsalpinia, a Leguminous genus, containing two wide-ranging shore species. Speaking generally the rule applies; and I found in Fiji that whilst the seeds of the two littoral plants (C. Bonducella and C. Bonduc) were as a rule buoyant, those of an inland mountain species sank. But it is very remarkable that although the seeds of C. Bonducella have long been known to be transported by the currents, and are often stranded by the Gulf Stream on the coast of Scandinavia, when it grows in Hawaii, where it is as a rule an inland plant, the seeds lose their buoyancy. This is quite in accordance with the general principle; but I must refer the reader for a general treatment of this genus to Chapter XVII. There also will be found the instance of another Fijian littoral plant, Afzelia bijuga, a common littoral tree with buoyant seeds which also lose their buoyancy when the tree grows inland. A similar instance is afforded by Kleinhovia Hospita, the seeds of which seem to lose their buoyancy in inland stations. Not all littoral plants, however, lose the floating power of the seeds when grown away from the coast. The seeds of Ipomea pes capræ retain it in spite of the change of station. This point is dealt with in Chapter XIII and in Note 44.

In concluding this general sketch of the first results obtained by testing the buoyancy in sea-water of a collection of seeds and fruits from a mountainous Pacific island, such as we find in Fiji, I must remind the reader that the subject has only been lightly

treated. Enough, however, has been said to illustrate the character of the sorting-process by which in the course of ages the plants with buoyant seeds or seedvessels have been gathered at the coast. This is indicated :—

(1) By the far greater proportion of species with buoyant seeds and seedvessels amongst the shore plants than among the inland plants.

(2) By the circumstance that almost all the seeds or fruits that float unharmed for long periods belong to shore plants.

(3) By the fact that when a genus has both inland and littoral species, the seeds or fruits of the coast species as a rule float for a long time, whilst those of the inland species either sink at once or float only for a short period.

These results, therefore, justify our dividing the flora of our island into two groups, the one including the plants with buoyant seeds or fruits and comprising most of the littoral plants, the other including the plants with non-buoyant seeds or fruits, a group which contains almost all the inland plants and indeed nine-tenths of the flora. This classification is a very crude one; but it enables us at once to assign a value to the agency of currents in stocking a Pacific island with its plants. Yet this is but the initial step in an inquiry that branches off in a thousand different ways, even if restricted to the littoral plants. There are a host of difficulties connected with the history of the strand-flora of such an island which can only be properly gauged when viewed from various standpoints.

CHAPTER III

THE LESSON OF THE BRITISH FLORA

Results of observations on the buoyancy of over 300 British plants.—The small proportion of plants with buoyant seeds or seedvessels.—Their station by the water-side.—The great sifting experiment of the ages.—Summary.

THE singular relation between station and seed-buoyancy that exists in an island of the tropical Pacific, such for instance as Vanua Levu, Tahiti, or Hawaii, would lose much of its significance if it stood alone in the economy of plant-life. It must be true not only of tropical floras generally, but of those of the temperate regions; and there can be little doubt that it prevails all over the world. Displayed to us at first in a Pacific island, it acquires a new significance when we study it in the light of numerous observations made in Europe. It exhibits itself then as part of a far wider method pursued by Nature in determining the stations of plants. It is not only at the coast, but also at the river-bank and at the lake-side that Nature "locates" the plant with the buoyant seed or seedvessel. This relation is indeed as well exhibited in inland districts as it is at the coast.

In this connection I have the results of my own investigations on the buoyancy of the seeds and fruits of British plants and on the composition of the seed-drift of ponds and rivers, which were carried on in the years 1890—96. Some of them were published in a short paper on the seed-drift of the Thames, read before the Linnean Society of London in June, 1892, and in the columns of *Science Gossip* for April, May, and October, 1895; but the mass of the observations remain in my notebooks. Nor do my observations of the period since elapsed lead me to alter the position then adopted. I have since pursued the same line of inquiry in Hawaii,

Fiji, on the Pacific coast of South America, and in Sicily, and with the same results.

Since the elaboration of my notes was begun in 1900, Dr. Sernander, the Swedish botanist, has published (1901) his work in Swedish on the Dispersal-biology of the Scandinavian plant-world, in which the seed-drift of river, pond, and sea is exhaustively treated. Although this author has dealt with plant-dispersal from a somewhat different standpoint, I have perused his pages with the keenest interest and with great profit, having gone over much of the same ground with respect to the seed-drift of ponds and rivers. Yet the introductory remarks to my paper in *Science Gossip* in 1895 are as apposite now as they were then, and the reader will, I trust, pardon my reproducing them.

"By following up the path of inquiry that is concerned with the flotation of seeds and seedvessels, we are guided into other fields of research that give promise of interesting discoveries in connection with plant-life. We are led in the first place to consider the question of utility, and to ask whether the buoyancy of the seed or fruit has been a matter of moment in the history of the species. Nature is ever engaged in telling off the plants to their various stations. She places the yellow iris at the river's side and assigns to the blue iris its home in a shady wood. Under her direction the common alder thrives at the water's edge, whilst its fellow species live on the mountain slope. These and similar operations are carried on daily around us, and we know but little of the wherefore and the how. We are induced, therefore, to inquire whether by pursuing the line of investigation above indicated we may be able to get a glimpse at the methods adopted by Nature in selecting stations for plants."

I possess the results, which are given in Note 10, of buoyancy experiments and observations on the seeds and seedvessels of about 320 British flowering plants belonging to about 65 families. Of these about 260 are included in my own results, the data for the rest being obtained from the writings of Darwin, Martins, Thuret, Kolpin Ravn, and Sernander. In the great proportion of cases, 240, or 75 per cent., sinking took place at once or within a week; whilst 80, or 25 per cent., floated for a longer period, usually a month or more; and about 60, or nearly 20 per cent., floated for several months. It is to this last small group that belong the seeds or seedvessels that float through the winter in our ponds and rivers.

If the grasses had been properly represented, the grains of which possess as a rule but little buoyancy, except through air-bubbles

temporarily entangled in the glumes, the proportion of seeds and fruits that sink at once or in a few days would probably have been about 80 per cent. Then again, since the plants from stations where buoyant seeds and seedvessels are most frequently found—that is at the river-side, the pond-margin, and the sea-coast—are much more completely represented in these experiments than those from other stations, it would seem that even 80 per cent. is too low a figure. Even if the 80 plants with the buoyant seeds or seed-vessels included all the species thus characterised, which they certainly do not, we should obtain an estimate for the British flora (rather over 1,200 species of flowering plants) of about 93 per cent. with non-buoyant seeds or fruits. This is, of course, too high. It is, however, very probable that the proportion of plants with non-buoyant seeds or seedvessels for the whole British flora is about 90 per cent.

This proportion of plants with non-buoyant seeds or seed-vessels, that is to say, of those that sink at once or within a week, is also approximately correct for the flora of one of the larger islands of the tropical Pacific. The data at my disposal only enable me in the cases of Fiji and Hawaii to fix it at between 95 and 85 per cent., or on an average 90 per cent. With the floras of continental regions the proportion would doubtless be markedly higher. That seeds and seedvessels as a rule possess but little buoyancy was a sound conclusion of Darwin, and one, as he remarked, that is in accordance with the common experience of gardeners. Thuret, after experimenting on the buoyancy in sea-water of the seed or seedvessels of 251 species of plants, belonging to 77 families and to various regions, found that scarcely two per cent. had any powers of flotation, all the rest sinking at once or in a few days, a result that led De Candolle in a note to this memoir to reiterate his opinion regarding the inefficacy of currents as plant distributors. Thuret, however, did not select many of his plants from stations where buoyancy is most frequently exhibited, and his estimate errs, therefore, in imputing too little buoyancy to seeds in general. The power of seeds and fruits to germinate after prolonged flotation in sea-water has long been well established, and it is often illustrated in this work, so that there is no need to dwell upon it here. (See Note 11.)

Of the 240 species of British plants where sinking took place at once or within a week, in about 50 per cent. the plants had dry indehiscent fruits, such as we find in the genus Ranunculus and in

the Umbelliferæ, the Compositæ, and the Labiatæ; whilst in about a third the plants had dehiscent fruits with small seeds, such as are characteristic of the Cruciferæ, the Caryophyllaceæ, and the Juncaceæ. Plants with large seeds, such as those of Nuphar luteum and Convolvulus arvensis, make up only six per cent. of those of the non-buoyant group, the remainder comprising plants with berries, such as Solanum, and others with miscellaneous fruits.

Of the 80 plants where the seeds or fruits floated more than a week, usually for several weeks, and often for months, 70 per cent. possessed dry, indehiscent fruits, such as those of Hydrocotyle vulgaris, Bidens cernua, Lycopus europæus, Carex, &c., whilst only 6 or 7 per cent. had dehiscent fruits with small seeds, such as we find in Lysimachia and Menyanthes, the remainder being generally characterised by large seeds, such as those of Convolvulus sepium, C. soldanella, Iris pseudacorus, Calla palustris, &c. It would thus appear that, in so far as buoyancy is concerned, Nature has for the most part ignored the small seed and has confined herself mainly to the dry indehiscent fruit. We have already seen that this is also true of the same great sorting-process in the tropical islands of the Pacific, and it doubtless applies all over the world.

We have now to learn the significance of this distinction amongst British plants between those with and those without buoyant seeds or seedvessels. When we regard the stations of these 80 plants of the buoyant group we find that about 70 per cent. of them are placed by the river, or the pond, or the sea, the fresh-water stations much predominating. But if we include the plants of the moist meadows adjoining the rivers, such as Ranunculus repens, Rhinanthus crista galli, some Cyperaceæ, &c., the buoyant fruits or seeds of which are regularly swept into the stream in the time of flood, we shall raise the proportion possessing a water-side station to 80 per cent. On the other hand, about two-thirds of the 240 plants of the non-buoyant group, which are enumerated in Note 10, live away from the water-side; but the proportion of plants with a relatively dry station would be considerably higher than this figure for the whole flora, since my investigations were especially directed towards plants frequenting wet stations, and the number of them is excessive in the list.

Supposing, however, that our materials were restricted to the 260 plants tested by myself, we should obtain highly instructive results, since in a general sense the floating powers of their seeds or fruits were tested to the finish. We place them, let us say, in a bucket of water, and after six months we find that in not more

than forty plants are the seeds or seedvessels still afloat. These forty plants, excluding two or three littoral plants, are nearly all plants of the borders and vicinity of rivers and ponds. (They are indicated in the list given in Note 10 by the numbers vi. and xii., the last being those where the flotation experiment was prolonged to a year and over.)

It would thus seem—I am now quoting mainly from my paper in *Science Gossip* for May, 1895—that there are gathered at the margins of rivers and ponds, as well as at the sea-border, most of the British plants that could be assisted in the distribution of their seeds by the agency of water. This great sifting experiment has been the work of the ages, and we here get a glimpse at Nature in the act of selecting a station. But the curious character of the sorting process becomes yet more apparent when we discover that the buoyancy of the seeds or fruits of species of the same genus may become a matter of station.

We will first take the four British species of Stachys (arvensis, betonica, sylvatica, and palustris). Of these the fruits of S. palustris alone possess any buoyancy, being able to float for weeks. It is the only species that finds its characteristic home at the water-side ; and as observed by Sernander its reproductive shoots occur in the Scandinavian fresh-water drift.

Galium illustrates the same principle. Whilst in my experiments the fruits of G. aparine and of another species growing in a dry station displayed little or no floating power, those of G. palustre, which alone grows at the water-side and in wet situations, have great buoyancy. As my observations show, they float unharmed through the winter in our ponds and rivers, and, according to Sernander, are often found in the Baltic sea-drift. (See Note 12.)

The achenes of Potentilla afford another example. Those of P. tormentilla and of another species from dry situations have but little floating power. On the other hand, those of P. comarum float indefinitely. The last also came under my notice in the floating drift of ponds in February ; and we learn from Sernander that they occur in the fresh-water and salt-water drift of Scandinavia.

As a further instance, I will take the two British species of Iris. The familiar river-side Iris pseudacorus has seeds that float unharmed in our ponds and rivers from the autumn to the spring, and often for a year or more. On the other hand, the seeds of Iris fœtidissima, which has its home in the shady wood, sink at once even after drying for months.

The nature of the sorting-process is especially well shown in some of the families, as for instance with the Labiatæ. Let the reader put on one side the four species with buoyant fruits, namely, Lycopus europæus, Mentha aquatica, Scutellaria galericulata, and Stachys palustris, and on the other side all the species with non-buoyant fruits, such as Salvia verbenaca, Thymus sp., Calamintha officinalis, Nepeta glechoma, N. cataria, Prunella vulgaris, Stachys arvensis, S. betonica, S. sylvatica, Galeopsis tetrahit, Ballota nigra, Lamium purpureum, L. album, Teucrium scorodonia, and Ajuga reptans, and he will at once perceive that he has separated the regular water-side plants from those growing in drier stations.

If he does the same with the Umbelliferæ he will find that when he is separating Hydrocotyle vulgaris, Cicuta virosa, Œnanthe crocata, and Angelica sylvestris from Æthusa cynapium, Pastinaca sativa, and Chærophyllum sylvestre, on account of their buoyant fruits, he is also distinguishing them on account of their stations. On the other hand, there are apparently weighty exceptions to this rule in the non-buoyancy of the fruits of the three British species of Apium (graveolens, nodiflorum, inundatum), which grow in streams and marshes. Or, again, if we look at the sea-coast representatives of the family, we find that whilst the fruits of the Samphire (Crithmum maritimum) float buoyantly for months, those of Eryngium maritimum seemingly set the law at defiance, and all sink in less than a week or ten days, even after months of drying. To regard these as exceptions, however, is to miss the essential point of the principle concerned. It is not thereby implied that all water-side plants, whether by the sea or by the river or by the pond, have buoyant fruits or seeds, but that nearly all plants with such fruits or seeds have been gathered at the water-side. It will be shown in the next chapter that several other influences go to determine the station of a plant on a beach or by a river. This is true of the Compositæ, which, if we except our two species of Bidens (cernua and tripartita), come under the play of other determining causes, as indicated by the little or no buoyancy displayed by the fruits of Aster tripolium, Senecio aquaticus, and Carduus palustris.

Within the limits of a genus we can, however, point to other examples of this principle. Take, for instance, Convolvulus arvensis, the common weed of our fields. Its seeds, whether fresh or dried for months, have no buoyancy. On the other hand, those of Convolvulus soldanella float unharmed in sea-water for half a year and more. Its seeds have come frequently under my notice among

the stranded drift of the Devonshire beaches, and also on the coasts of Chile; whilst Sernander includes them amongst the drift of the beaches on the Norwegian coasts. It is remarkable that Convolvulus sepium, which accompanies C. soldanella over much of its great range, has seeds that are sometimes able to float unharmed for long periods, even for years (Notes 13, 41, 49). Though not strictly a water-side plant, it grows commonly over other plants on the banks of the Thames; and when it fruits its seeds occur typically in the floating drift of that river. According to Gray, it is almost a river-side plant in the United States, where it is found "especially on the moist banks of streams." Not all the seeds of C. sepium, however, are buoyant; and in its varying behaviour in this respect it resembles the inland species of Ipomea, which are referred to in the previous chapter.

The British species of Euphorbia also seem to behave in accordance with the principle that when a genus has littoral and inland species, the first-named alone possesses buoyant fruits or seeds. Thus, whilst the sound fruits of E. helioscopia and of another species found commonly as a garden weed are non-buoyant, those of E. paralias, the familiar beach-plant, float for several weeks, and are to be noticed among the stranded drift of the coasts frequented by this plant. (See Note 90 for later results.)

The structural characters connected with the buoyancy of the seeds or seedvessels of some of the British plants are dealt with in Chapter XII. Here it may be remarked that this capacity is often associated, as with the Pacific island plants, with a "buoyant" tissue, that is either absent or less developed in the case of the non-buoyant group.

Enough has now been said to show in a general fashion how Nature through the agency of buoyant seeds and fruits has affected the stations of plants of the British flora. Allowing this line of inquiry to develop itself as the work proceeds, we will here pause and close the chapter with a reference to some of the principal points that have been brought into prominence.

(*a*) The proportion of flowering plants of the British flora that possess buoyant seeds or seedvessels is very small, probably not more than 10 per cent.

(*b*) In so far as buoyancy is concerned, Nature has for the most part ignored the dehiscent fruit with small seeds, such as we see in the Cruciferæ and the Caryophyllaceæ, and has chiefly endowed with floating power the dry indehiscent fruit, such as we see in the Umbelliferæ and in the Labiatæ.

(*c*) In the great sorting-process that has been in operation through the ages, nearly all the plants with buoyant seeds or seed-vessels have been located at the water-side, principally by ponds and rivers, but also on the sea-beach. On the other hand, the great majority of the plants with seeds or seedvessels that sink have found a home in drier stations.

(*d*) The character of the operation is well displayed in certain genera possessing species of the water-side and species of drier situations, and in the case of genera having both coast and inland species. In both instances the species by the water-side possesses buoyant seeds or fruits, whilst that of the station in a drier locality or removed from the coast has seeds or fruits that sink.

(*e*) Yet it is necessary to remember that the principle involved is not that all water-side plants have buoyant seeds or fruits, but merely that plants thus endowed gather at the water-side. There are many plants with non-buoyant seeds or fruits on our beaches and beside our ponds and rivers.

(*f*) We have now learned from the British flora that the "locating" of plants with buoyant fruits or seeds on the beaches of the tropical islands of the Pacific, and indeed of tropical regions generally, is but a part of a much wider principle by which plants thus endowed are placed at the water-side, whether by a river or a pond or by the sea.

(*g*) It is with this distinction between a fresh-water and a salt-water station that we shall be occupied in the next chapter; and it is of great interest, since it leads us to discover that the wider principle is in its turn part of a far larger scheme.

Note.—It must be clearly understood that by water-side plants the true aquatic plants, such as the Water-lilies, the Myriophylls, the Potamogetons, &c., are not implied. It will be seen from the list in Note 10 that in most cases the seeds or fruits of aquatic plants have little or no floating power. This is true, for instance, of Ranunculus aquatilis, Nymphæa, Nuphar, Myriophyllum, Ceratophyllum, Callitriche, Naias, Zannichellia, Ruppia, and half the Potamogetons.

CHAPTER IV

THE LESSON OF THE BRITISH FLORA (*continued*)

The choice of station of the water-side plant possessing buoyant seeds or seed-vessels.—Determined by its fitness or unfitness for living in physiologically dry stations.—In the internal organisation of a plant lies the first determining influence of station.—The grouping of the British strand-plants.—Whilst the Xerophyte with buoyant seed or fruit finds its station at the coast, the Hygrophyte similarly endowed makes its home at the river or pond side.—The grouping of the plants of the river and the pond.—Summary.

BY following up the clue supplied by the floating seed, we have arrived at the conclusion with respect to the British flora that plants with buoyant seeds or fruits gather at the water-side. But we have yet to inquire why some of these plants are "located" at the sea-coast and others on the borders of ponds and rivers. Mere buoyancy aided by chance has not determined the choice. There are definite principles at work in the economy of plant-life that make the selection for each plant.

Rivers in all parts of the world carry to the sea in great abundance the seeds and fruits of the plants that are stationed at their borders; and such seed-drift is found in quantity washed up on the beaches in the vicinity of the estuary. One finds, for instance, on such beaches in the South of England the stranded fruits and seeds of Bidens cernua, Alnus glutinosa, Sparganium ramosum, Iris pseudacorus, &c., mingled with those of true beach plants like Cakile maritima, Convolvulus soldanella, Euphorbia paralias, &c. Yet we would be much surprised if either the Bidens or the Alder or the Sparganium were to establish itself on the sandy beach, even though they have had through the ages innumerable opportunities of doing so. We thus see that mere

buoyancy of fruit or seed cannot determine a station on a sea-beach, and that some other factor makes the choice. The nature of this factor I will now endeavour to explain; but in so doing it will be necessary to employ a few technical terms, which it is not easy to dispense with altogether.

It may be doubted whether Professor Schimper could have conferred a greater benefit on the student of plant-distribution than in his clear delineation of the connection between the habit or organisation of a plant and its station. Nature has imposed an important structural distinction between plants that have been endowed with the means of checking excessive transpiration or water-loss in stations where there is risk of drought, as in deserts and in similar arid localities, and those that live in stations where such safeguards are not needed. Hence arises the distinction between Xerophytes on the one hand, and Hygrophytes on the other. This contrast is shown not only in minute structural features, but also, as my readers are aware, in the external characters, as in hairiness, succulency, a leathery cuticle, the occurrence of thorns, and in several other characters of the plants of the steppe and the desert. This important subject is dealt with by Professor Schimper in his recent work on Plant-Geography; but it was from his earlier work on the Indo-Malayan strand-flora that I learned this valuable lesson in plant-distribution.

It has been ascertained, however, that a safeguard against excessive water-loss by transpiration is not only needed by plants living in arid localities, but also by those placed at the coast. Both the shore plant and the plant of the steppe and the desert present the same xerophilous organisation, provision against excessive transpiration being also required by the beach plant to prevent the injury of the green cells from the accumulation of salt in the tissues. It would thus appear that plants of the Hygrophytes that possess buoyant seeds or fruits are gathered at the borders of ponds and rivers, whilst those of the Xerophytes that are similarly endowed find their station on the sea-shore. This important distinction penetrates very deeply into the conditions defining the stations of plants. The connection between the plant of the coast and the plant of the steppe or the desert is strikingly shown on those occasions when the beach plants extend inland over parched and arid plains, such as occurs for instance in North Africa, and in the larger islands of Fiji, as described in Chapter V.

The causes of the buoyancy of fruits and seeds, as pointed out

in Chapter XII, are so various, that it appears at first sight impossible to connect them with the xerophilous or hygrophilous organisation of a plant, or, in other words, with any structural characters associated with particular stations; yet behind all lies the general principle that, given a plant of the buoyant group, if it is a Xerophyte it finds its way to the coast, and if a Hygrophyte it makes its home by ponds and rivers. In the case of a tropical littoral flora, such as we find in a Pacific island, the large proportion of plants with buoyant fruits or seeds gives so much prominence to the subject of their distribution by currents that the question of "station" is often masked. On the other hand, in the shore-flora of a temperate region like that of Great Britain, the plants with buoyant seeds or fruits are in the minority, and the question of "station" is the first to obtrude itself.

In establishing the principle that most of the plants with buoyant seeds or fruits have been gathered at the water-side, it was never implied that all the plants by the river or by the pond or at the coast are thus characterised. There is much to learn from the circumstance that whilst nearly all plants with buoyant seeds or fruits are placed at the water-side, not all water-side plants have buoyant seeds or fruits. In the first place, it is to be inferred in the light of what has been said above that the first determining principle in the selection of a station is concerned not with the buoyancy of the seeds or fruits, but with the xerophytic or hygrophytic organisation of a plant. In other words, it is the fitness or the unfitness of a plant for living in situations where the loss of water by transpiration requires to be checked that primarily determines the station at the coast. We thus see in the internal organisation of the plant the primary determining influence on station. Buoyancy of seed or fruit comes subsequently into play, the Xerophyte and the Hygrophyte, thus endowed, ultimately finding their way, the first to the beach, the second to the bank of the river or to the margin of the lake or pond.

In the next place, when we regard the composition of the British coast-flora, and examine the distribution of the plants in other situations than on the beach, we obtain some interesting results. There is first a group of plants, including such as Armeria vulgaris, Artemisia maritima, Cochlearia officinalis, Erodium maritimum, Matricaria inodora, Plantago coronopus, Polycarpon tetraphyllum, Raphanus maritimus, Spergularia rubra, Silene maritima (see Note 15), and others, all of which occur not only at the coast and on the adjacent hill-slopes, but also often far inland, and

sometimes at considerable elevations in mountainous districts, as in Central Europe. It is on this occurrence of certain shore-plants in alpine regions that Prof. Schimper lays much stress in his memoir on the Indo-Malayan strand-flora (p. 28), and in his later work on Plant Geography (Engl. edit., p. 716), when pointing out that here temperature does not play a determining part, and that in both stations, whether on the sandy beach or on the mountain-top, the same xerophilous organisation is needed to obviate the risk of impeded water-supply. He quotes in this connection the observation of Battandier that many alpine species from the Atlas Mountains occur on the Algerian beaches, but not in intervening regions. Mr. Druce, in his discussion of the British species of Sea-Thrifts and Sea-Lavenders (Armeria, Statice), brought the subject of the occurrence of maritime plants on mountain summits again to the front; but he did not advance any general explanation, and seems to regard it as the result, as it doubtless is, of the recurrence of suitable stations (*Jour. Linn. Soc. Bot.*, Dec. 1900).

Very few of these plants have any capacity for dispersal by currents, a subject dealt with in Note 16. Several of them have dehiscent, small-seeded fruits which, as pointed out in the previous chapter, hardly ever come into the buoyant category. I have experimented on the greater number of them, and in only one species, Matricaria inodora (var. maritima), do the results indicate a capacity for dispersal over wide tracts of sea.

If we look again at a list of British shore-plants, we find another group of plants frequenting salt marshes and muddy shores, and found also often far inland, as in the saline plains of Central Asia. Here we have such plants as Aster tripolium, Glaux maritima, Plantago maritima, Salicornia herbacea, Salsola kali, Samolus valerandi, Scirpus maritimus, Suæda fruticosa, S. maritima, Triglochin maritimum, T. palustre, &c. It becomes in this connection a subject of peculiar interest to the student of plant-distribution when he reads in Mr. Hemsley's paper on the flora of Tibet (*Jour. Linn. Soc. Bot.*, vol. 35) that amongst the British shore-plants above-named the two species of Triglochin and the same species of Glaux and Salsola occur in the salt marshes of the Tibetan uplands at elevations of 15,000 to 16,000 feet, Scirpus maritimus also being found in the swamps of the lower levels. We have the same thing, affecting much the same plants, illustrated in America. Thus we learn from Asa Gray that Salicornia herbacea, Scirpus maritimus, Triglochin maritimum, &c., which are common in salt

marshes on the coast of the United States, occur also in the interior of the continent in the vicinity of salt-springs.

Facts of this sort are well known, and I merely refer to them here in order to emphasise the importance of this little group of British littoral plants, those of the salt marsh. Their very wide distribution is connected with the frequent recurrence of suitable conditions, not only in space, but what seems of greater import, also in time. One can scarcely doubt when the Saltwort (Salsola kali) is seen on the Devonshire coast, on a beach in Chile, and in the elevated regions of Central Asia that here a very ancient type of plant finds its still more ancient conditions of existence. In the capacity which most of the plants of the salt marsh possess of germinating in sea-water, this group of littoral plants is sharply distinguished, as far as my observations show, from the other groups of British shore-plants. For instance, in my experiments the seeds of Aster tripolium, Salicornia herbacea, and Triglochin maritimum germinated freely in sea-water, whilst those of Spergularia rubra, Cakile maritima, Convolvulus soldanella and others failed to do so (see Note 19). It will also be noticed with respect to this group of littoral plants that, except in the case of Scirpus maritimus, the seeds or fruits have little or no floating power, the exception offered by Salsola kali being not very striking. This feature is brought out in the Table given in Note 10; but some of the details of my observations are given in Note 17.

There yet remains a third group of the British shore-plants, namely, that comprising the plants that rarely stray far from the beach and often possess seeds or seedvessels that will float for months. Here we have such species as Arenaria (Honckeneya) peploides, Beta maritima, Cakile maritima, Crambe maritima, Crithmum maritimum, Convolvulus soldanella, Eryngium maritimum, Euphorbia paralias, Glaucium luteum, Lathyrus maritimus, Polygonum maritimum, &c. The seeds or seedvessels of quite half of these species will float for months unharmed in sea-water, but in a few, as with Cakile maritima and Eryngium maritimum, they float for only a week or two, whilst in others again like Glaucium luteum they have no buoyancy. (Some details of the buoyancy experiments on these plants are given in Note 18; and the long list in Note 10 may be first consulted.)

It is not necessary to enter here into more detail with respect to British shore-plants. Enough has been said to disclose cleavage-lines in what might have appeared as a homogeneous plant-formation. We can thus discern the elements of at least three groups

amongst the plants of our beaches, each group bearing the impress of an independent history :—

(*a*) The plants of the beach and of the inland plain or of the distant mountain peak, excluding those of the salt marshes. Armeria vulgaris, Silene maritima, and Spergularia rubra may be taken as examples. The currents here as a rule take little or no part in their dispersal.

(*b*) The "saline" group, including the plants of the saline plains and the salt marshes of the interior of continents. Of these Glaux maritima, Salsola kali, and Triglochin maritimum are examples. The capacity of germinating in sea-water is a distinguishing character of most of the plants ; and but few of them possess seeds or seedvessels that are markedly buoyant.

(*c*) The true beach plants that rarely stray far from the beach, of which Arenaria peploides, Cakile maritima, and Convolvulus soldanella are examples. Many of them have buoyant seeds or fruits capable of dispersion over wide areas through the agency of the currents.

The reader will be able to extend this subject for himself if he is so inclined, but we have gone far enough together to learn that the plants with buoyant seeds or fruits are in the minority on our beaches, scarcely a third of the total being fitted for dispersal by the currents over broad tracts of sea. The British strand-flora thus differs strikingly from the littoral flora of a Pacific island, or indeed of any ordinary tropical coast, and in this respect it is to be regarded as typical of the temperate regions. It has been remarked before that on a beach in the tropics we would expect to find that quite three-fourths of the plants are provided with buoyant fruits or seeds distributed far and wide over the tropical seas by the currents.

We pass on now to briefly discuss from the same standpoint the British plants that find their homes on the borders of rivers and ponds. It is here that the hygrophytes with buoyant seeds or fruits gather together, just as the xerophytes with similar seeds or fruits collect on the beaches. We have seen before that only a portion of the beach plants belong to the buoyant group, and the same applies to the plants at the edges of rivers and ponds. The plant-formation is no more homogeneous there than it is in the case of the strand-flora. Let us see if we can discern some lines of division there also, or in other words let us endeavour to connect the absence or presence of floating power in the fruits and seeds with some variations in the placing of the plants. We still pursue

the clue to the study of the complicated problems connected with plant-stations by taking the floating seed as our guide.

We will carry ourselves in thought to the Thames-side between Teddington and Twickenham at the end of August, 1892. The river is at the high-water level, and we see flourishing at the margins, sometimes a little above the water and sometimes a little within its reach, Ranunculus repens, R. sceleratus, Spiræa ulmaria, Lycopus europæus, Scutellaria galericulata, different species of Rumex, Alnus glutinosa, Iris pseudacorus, Sparganium ramosum, and different species of Carex, with several other plants, all contributing their seeds or fruits to the drift that floats in the river from the autumn to the spring.

But besides these plants there are a number more or less submerged in the stream, including Nasturtium amphibium, N. sylvestre, Stellaria aquatica, Myosotis palustris, and Veronica beccabunga; and as the water falls other plants still more submerged come into view on the exposed flats, such as Nasturtium officinale, Apium nodiflorum, and Polygonum hydropiper. None of these plants are represented by their seeds or fruits in the floating river-drift. Several of them possess dry dehiscent fruits with small seeds, such as Nature ignores in the matter of buoyancy, and the small fruits of Myosotis, Apium, and Polygonum have little or no floating power.

We have thus here a clear dividing line between the plants with buoyant seeds or fruits that were more or less exposed above the high-water level, and those that were more or less submerged at that state of the tide. That which occurs in the Lower Thames twice in the day within the reach of the tide represents what happens in the higher part of the river during the seasonal floods, but in the last case the effects cannot be so readily distinguished. We thus perceive that the buoyant seed or fruit is as a rule only characteristic of the plants of the river-side that grow more or less exposed above the water, whilst those plants liable to periodic submergence have seeds or fruits that sink.

In this connection it is of especial interest to observe that as a general rule the truly aquatic plants of English rivers contribute little or nothing to the floating seed-drift. I pointed this out several years ago, in my paper on the Thames, as an agent in plant-dispersal, and it has been already noticed in this work (page 30). We look in vain amongst the floating winter drift of our rivers for the seeds or fruits of Ranunculus aquatilis, Nuphar luteum, Nymphæa alba, and of the species of Myriophyllum, Limnan-

themum, Callitriche, Ceratophyllum, Zannichellia, and of several of the Potamogetons, all of which give character in summer to the aquatic vegetation of the river. In their place we find only the seeds and fruits of the plants growing on the banks.

There is, however, another small group of river plants, which in their structure and habits and in the behaviour of their floating fruits come between the true aquatics and the plants of the river-banks. They belong mostly to the Alisma family, and Alisma plantago and Sagittaria sagittifolia may here be specially mentioned. Their fruits display great variation in their floating power; and on this point M. Kolpin-Ravn, writing to me in 1895, made the following interesting suggestion, that since these plants approach true aquatics in structure they may be also regarded as approaching them in the inconstancy of the buoyant capacity of their fruits, those of aquatics having typically little or no floating power.

Seed-buoyancy, however, does not play quite such an important part in the plant-economy of a river as the examination of the floating drift would lead one to expect. Only a portion of the bank-plants have buoyant seeds or fruits, whilst amongst the true aquatics, the semi-aquatics, and the plants periodically submerged, the rule of non-buoyancy prevails. And, indeed, when we look at all the possible stations for the plants of the British flora, we discover that seed-buoyancy can rarely be connected with station. It is, however, in those few stations that plants with buoyant seeds have mainly gathered. There it is, probably, that the remnants of a past floral age find a refuge, since it would seem likely that the tendency has been in the course of geological time for the development of dry stations for plants at the expense of the wet stations.

The following is a summary of some of the points discussed in this chapter :—

(1) In the case of the strand-flora of a Pacific island, and indeed in that of an ordinary tropical region, the large proportion of plants with buoyant seeds or fruits tends to mask all other issues, and we are seemingly only concerned with dispersal by currents.

(2) But in the British strand-flora where plants with buoyant seeds and fruits are in a minority, constituting less than a third of the total, it is seen that the issue is primarily an affair of station, an inference that may be applied generally to temperate regions.

(3) All British shore-plants may be regarded as owning certain characters in common which may be collectively designated the

xerophilous habit, and we may extend this view to other temperate strand-floras.

(4) But this xerophilous habit is also characteristic of inland plants in certain localities, as of those of the steppe, the desert, the rocky mountain-top, and of other exposed situations, in all of which checks to the loss of water by transpiration are required. Whilst the risks of drought are thus guarded against in the case of plants stationed in arid localities, the risk of injury to the plant from the accumulation of salt in the tissues is obviated in the instance of the plants of the coast.

(5) On the other side we have the hygrophilous habit characteristic of plants living under conditions where checks to transpiration are relatively little needed. All the plants of the margins of rivers and ponds belong here, and indeed all plants living under moist conditions.

(6) This distinction between the xerophilous and hygrophilous habits penetrates deeply into all questions connected with stations, and lies behind all matters relating to the buoyancy of seeds or fruits. It is the fitness or unfitness of a plant for living in dry situations that primarily determines the station. If a xerophilous plant has a buoyant seed or seedvessel it finds its way ultimately to the coast; if it is hygrophilous and its seeds or fruits can float, then it is finally established on the side of a pond or river.

(7) The composite character of the British strand-flora is to be explained on the above principles. We have in the first place the plants confined to the sandy beach, many of which possessing buoyant seeds or fruits are dispersed by the currents. Next come the plants of the sandy beach which are found also far inland in open plains and on mountain-tops; and afterwards come the plants of the salt-marsh and mud-flats of the coast, which appear again in the saline plains and swamps in the interior of the continents.

(8) The plant-formation of the river's border displays also lines of division, and is by no means homogeneous; and indeed other factors besides those connected with seed-buoyancy have here been in operation.

(9) In only a few of the possible stations of British plants can a direct connection be traced with seed-buoyancy. Yet it is at these few stations, such as at the coast and by the pond or river, that the plants with buoyant seeds and fruits have mainly gathered.

(10) The plants now frequenting wet stations may often be regarded as the remains of an age when moist conditions for plant-life prevailed.

CHAPTER V

THE FIJIAN STRAND-FLORA

The inland extension of the beach plants.—The grouping of the coast plants.—Their modes of dispersal.—The zone of change.—Summary.

HAVING learned from the British flora the real significance of the buoyant seed or fruit in a littoral flora, we will now return to the Pacific and proceed to deal with the composition and general character of the strand-plants.

Speaking of the Malayan strand-plants, Professor Schimper remarks (pp. 11, 12) that both in outward appearance and in anatomical structure they are xerophilous in character, whether in the case of those of the mangrove-swamp or in those of the beach. Since the tropical shore-flora of the Pacific islands is essentially Malayan, the identity usually extending to the species, the same conclusion may be applied to its character. The xerophilous habit may show itself externally in a variety of ways, as in hairiness, leaf-structure, a leathery cuticle, succulency, &c.

From this xerophilous habit of the Pacific strand-flora we should expect to find that many of the plants stray far from the coast, wherever the suitable conditions for their type of organisation occur, whether in the inland plain or on the mountain-top. This is indeed the case; but in dealing with this subject it will be necessary to discuss in some general detail the littoral floras of the Fijian, Hawaiian, and Tahitian groups in succession.

THE FIJIAN STRAND-FLORA

THE INLAND EXTENSION OF THE BEACH PLANTS

Viewed from the old standpoint of "station," where one would distinguish sharply between the coast and the inland plants, the Fijian strand-flora exhibits a number of inconsistencies, all at first

sight extremely puzzling. When, however, we regard their xerophilous character and reflect that this habit, and not mere fitness for growing at the coast, is the primary determining factor of their station, much that is strange appears normal and plain.

Let me refer in this connection to the impression that the distribution of the Fijian shore-plants made on Mr. Horne, the director of the Botanic Gardens of Mauritius, who spent a year in the botanical investigation of the group about a quarter of a century ago. In his account of the group (pp. 59, 60) he says that several of "what are known as sea-shore plants" are found far in the interior of the larger islands; and amongst others he names such characteristic beach plants as Cerbera Odollam, Hibiscus tiliaceus, Ipomea pes capræ, and Pandanus odoratissimus. On the other hand, he remarks that several species of inland plants occur at the coast, and that several plants growing on the mountain-tops are found near the sea. This apparent confusion of station he seems to attribute to the circumstance that the mountains of Fiji are not high enough for the development of an alpine flora. But such a view could not be held now, since the effect of an alpine flora would be the introduction of further elements of confusion in the occasional occurrence of some of the alpine plants on the sea-coast, as we find in Hawaii.

Yet this apparent mingling of the littoral and inland floras in Fiji becomes intelligible when we perceive that the seeming confusion of station is mainly restricted to the xerophilous plants of the arid inland plains and of the bare mountain-tops. The rank humid forests that cover so much of the interior of the islands, and the luxuriant vegetation of the mountain-gorges, are not here concerned. Such a mingling occurs it is true under certain conditions; but in the general physiognomy of the flora the distinction between the shore and inland plants holds good. The same shore plants that are distributed far and wide over the Pacific here present themselves; and although some of them extend far inland, where the scantily-vegetated plains descend to the coast, this does not deprive them of the right of being still regarded as littoral plants.

Still, when we look at a fairly complete list of the shore-plants of Fiji, numbering in all about eighty, we perceive that about two-thirds of them also occur inland, either in Fiji or in some other tropical region; and if we reflect that many of the residue are plants of the mangroves that would not be found inland except under estuarine conditions, it becomes evident that with this

reservation there are very few littoral plants in Fiji that do not at times leave the coast.

Cæsalpinia Bonducella may be taken as a type of those shore-plants that stray far away from the coast, even into the interior of continents, since in India it reaches the Himalayas. Although Terminalia Katappa and Calophyllum Inophyllum often owe their existence inland in different parts of the tropics to man's agency, this cannot be said of most others, as Cassytha filiformis, Casuarina equisetifolia, Cycas circinalis, Ipomea pes capræ, Pandanus odoratissimus, Premna tahitensis, Tacca pinnatifida, Tephrosia piscatoria, Vitex trifolia, &c., when they occupy the extensive inland plains that slope to the coasts on the lee sides of the large islands of Fiji. Plants, like Hibiscus tiliaceus, are found in a Pacific island almost as frequently away from the beach as on the beach itself; and this is true of most other regions of the tropics where it occurs.

Other plants that appear to be altogether confined to the sandy beach in Fiji, break away on rare occasions from their usual station and appear on the bare rocky summits of hills near the coast, even though the hill-slopes are densely wooded. On such bare hilltops in Vanua Levu, varying from 500 to 1,100 feet in elevation, one is surprised at times to find shore creepers and climbers like Canavalia obtusifolia and Derris uliginosa associated with other beach-plants more frequently found inland, such as Tephrosia piscatoria and Vitex trifolia, and in the company of climbing species of Morinda and of small trees of Fagræa Berteriana. When the "talasinga" (sun-burnt) districts, as the Fijians term the plains on the north sides of the islands, extend a long distance from the coast into the heart of the island, they carry with them their peculiar vegetation and the intruding beach-plants up to considerable elevations above the sea. We then find familiar beach-plants like Cerbera Odollam and Ipomea pes capræ growing far inland at heights of 1,000 feet and over above the sea. (See Notes 20 and 21.)

One is never quite sure of the behaviour of shore-plants in Fiji when the "talasinga" plains lie behind the beach, since even Scævola Kœnigii, usually a steadfast beach-plant, occurs at times some miles inland. (See Notes 20 and 55.) There are, however, a few that never came under my notice inland, such as Pemphis acidula, Triumfetta procumbens, and Tournefortia argentea. The extension of sea-coast plants for any distance inland depends a good deal on the occurrence of scantily-vegetated plains, or of

scrub-covered, rolling country at the back of the beaches; and doubtless that which I have described in the case of Fiji is to be found in other tropical coast-regions. Professor Schimper informed me by letter that he had noticed a similar inland extension of the shore-plants in the Seychelles. . . . I have only here touched on this subject. In Notes 20 and 21 the reader will find further details of the inland extension of the beach-plants, and in Note 22 is given a general account of the "talasinga" plains, in which the wandering beach-plants mingle with the peculiar vegetation of the plains themselves. Covered with reeds and bracken, and dotted over with clumps of Casuarinas and Acacias, with the Cycad and Pandanus distributed irregularly over their surfaces, such level districts possess, as remarked by Seemann, a South Australian look.

THE GROUPING OF THE FIJIAN LITTORAL PLANTS.

The littoral plants readily divide themselves into three principal groups as concerning their station, namely:

(*a*) The "beach-formation," typically exhibited on the whitish calcareous beaches of reef-bound coasts.

(*b*) The "mangrove-formation," found at intervals all along the coasts, but most fully developed at the estuaries, and for the most part occupying flats regularly overflown by the tide.

(*c*) The "intermediate formation," comprising the plants of the tracts between the beach and the mangrove-swamp and at the borders of the swamps.

This grouping does not differ materially from that adopted by Professor Schimper in the instance of the Indo-Malayan strand-flora. (See Note 23.)

To the beach-formation belong, amongst the trees and shrubs, Barringtonia speciosa, Calophyllum Inophyllum, Guettarda speciosa, Pemphis acidula, Scævola Kœnigii, Tournefortia argentea, &c., and amongst the creepers and procumbent plants, Canavalia obtusifolia, Ipomea pes capræ, Triumfetta procumbens, &c. To the mangrove-formation belong the Asiatic and the American species of Rhizophora, and species of Bruguiera, Carapa, Lumnitzera, &c. Amongst the trees that gather around the borders of the mangrove-swamp, constituting the intermediate formation, occur Barringtonia racemosa, Excæcaria Agallocha, Heritiera littoralis, Hibiscus tiliaceus, and several other species, all of them being equally at home on the sandy beach, at the border

of a mangrove-swamp, and on the banks of an estuary. The climbers, such as Entada scandens, Mucuna gigantea, Derris uliginosa, &c., belong more to the mangrove and to the intermediate formations than they do to that of the beach. Referring the reader to the more complete lists given in Note 24, I may remark that it is not always possible to distinguish sharply between the three formations, since some of the plants belong to two, and a tree like Cerbera Odollam may, in different localities, be referred to all three formations. The general distinction, however, prevails in the physiognomy of the coast-flora.

The mangrove-formation comprises, it may be pointed out, many plants other than mangroves, plants that find a home in the mangrove-swamps of Fiji, either within their limits or at their borders. It presents, indeed, a world in itself. When the mangroves establish themselves in a new locality they carry along with them a host of hangers-on, both plants and animals, that only find a home under the favourable conditions of a mangrove-swamp. Thus, the absence of the mangrove-formation from a Pacific island deprives its littoral flora of many very striking features. For this reason the Tahitian shore-flora must seem to a botanist coming from Fiji comparatively tame and monotonous; whilst that of Hawaii, for this and for other reasons to be subsequently mentioned, is still less interesting, and scarcely even gives a character to the coasts.

We are now, therefore, prepared to learn that a large number of the plants other than true mangroves, that thrive in or around the Fijian mangrove-swamp, are not to be found in those Polynesian islands where true mangroves do not exist; and that a law of association here exists. Many of the plants of the intermediate formation are so closely bound up with the mangroves in their life-conditions that they are not to be found where the mangroves are absent, even though their seeds or fruits are pre-eminently fitted for dispersal by the currents. The influence of "station" here rules supreme. This matter will be treated more in detail when discussing the Tahitian and Hawaiian strand-floras in Chapters VI. and VII.

THE MODES OF DISPERSAL OF THE FIJIAN STRAND-PLANTS.

The predominant influence of the currents having been already established, there remains for consideration the distribution of the floating capacity of the seeds or fruits among the different forma-

tions. One can say that almost without exception the seeds or fruits or seedlings of the mangrove and intermediate formations float for long periods. In the case of some of the true mangroves, as in Rhizophora and in Bruguiera, where germination takes place on the tree, it is the seedling that floats, whilst in others, as in Carapa and Lumnitzera, it is the seedvessel that floats. The plants with non-buoyant seeds or fruits that belong to the littoral flora are all confined to the beach formation, but they do not form more than a sixth of the total. Almost all the "good floaters" of the beach-plants are widely spread over the shores of the Pacific and of much of the tropics, and include such familiar species as Barringtonia speciosa, Cæsalpinia Bonducella, Terminalia Katappa, and many others mentioned in the lists of Notes 2 and 24.

When, however, we come to the dozen or so of beach-plants that possess seeds or fruits with little or no floating power, we find that several of them have a limited distribution in the Pacific, such as Acacia laurifolia, Drymispermum Burnettianum, Eugenia Richii, &c., whilst others, such as Casuarina equisetifolia, Tephrosia piscatoria, Triumfetta procumbens, and Wikstrœmia fœtida, are widely spread. This small non-buoyant group of the beach-plants has a nondescript appearance, and it is here that the inland flora is most likely to make its influence felt by additions to the number. It is here indeed that the littoral floras of the tropics mostly differ, the accessions from the inland flora varying in each region. It is in fact the zone of change.

A number of these plants, such as the species of Drymispermum, Eugenia, and Wikstrœmia, have probably been dispersed by frugivorous birds; whilst others, like Triumfetta procumbens, possess fruits that might have been transported in birds' plumage. From the frequency with which Tephrosia piscatoria is associated on hilltops in Fiji with Fagræa Berteriana and climbing species of Morinda that are well suited for dispersal by frugivorous birds, it seems likely that it is also distributed by birds fond of a drier diet. It is possible that the Polynesians, who much value the wood of Casuarina equisetifolia, have often assisted in dispersing the tree.

The following is a summary of the contents of the chapter.

(1) The extension inland of the Fijian strand-flora is to be attributed to the xerophilous organisation of the plants, and to the exceptionally favourable conditions that are offered to such plants on the plains, and in other scantily vegetated localities, lying usually on the drier sides of the larger islands.

(2) Excluding the mangroves and the plants associated with them in the coast-swamps, there are few littoral plants of the islands of the tropical Pacific that do not extend inland in one region or another.

(3) The Fijian shore-plants can be rudely arranged in three groups, those of the mangrove-swamp, those of the sandy beach, and those of the intermediate districts, the last including those plants that occur typically at the borders of a mangrove-swamp, though some of them can thrive equally well on a beach.

(4) There is a law of association connecting many plants with a mangrove-swamp in such a manner that when the true mangroves are not represented in a Polynesian group, as in Tahiti or in Hawaii, the plants in question are also absent, notwithstanding that in many cases, such as those of Clerodendron inerme and Heritiera littoralis, they possess seeds or seedvessels of great floating power.

(5) The fruits or seeds or seedlings, as the case may be, of the plants of the mangrove-swamp and of the bordering districts float almost without exception for long periods. This is true also of five-sixths of the beach-plants, whilst the remainder owe their dispersal chiefly to birds.

(6) The small non-buoyant group of the beach-plants represents that portion of the strand-flora that is most likely to be recruited from the inland flora. It is here that exists the zone of change; and it is in this respect that the littoral floras of the tropics differ principally amongst each other, the recruits from inland varying naturally with the floras of different regions.

Though it does not come within my plan to discuss the littoral floras of the adjacent smaller groups of Tonga and Samoa, it may be remarked that they reflect most of the principal features of the strand-flora of Fiji. In particular it may be observed that they possess the mangrove-formation, but to a more limited extent. Both own the mangrove genera Rhizophora and Bruguiera, whilst Carapa is also found in Tonga. The intermediate formation is represented in Tonga by Clerodendron inerme, Excæcaria Agallocha, and Heritiera littoralis; whilst in Samoa we find, besides the first-named species, Barringtonia racemosa and Scirpodendron costatum. In both the beach-formation is well represented.

CHAPTER VI

THE TAHITIAN STRAND-FLORA

(*From materials supplied mainly by the work of Drake del Castillo*)

Lacks the mangroves and their associated plants.—Possesses mainly the plants of the coral beach.—Predominant agency of the currents.—Inland extension of shore-plants.—Summary.

JUST as the littoral plants of Fiji may be regarded as typical of Western Polynesia, so the strand-flora of Tahiti, or, rather, of the Tahitian Islands, may be considered as representing Eastern Polynesia. We have thus the Tahitian area, comprising generally the Cook and Austral Groups, the Society Islands, the Paumotus, and also the Marquesas, as contrasted with the Fijian area, including the neighbouring Samoan and Tongan groups. For the sake of brevity the terms Fiji and Tahiti are often used as equivalents of the entire areas (see Note 25).

The littoral flora of this part of the Pacific lacks the mangroves and most of the plants that are associated in the Fijian region with a mangrove-swamp, either at its borders or within its interior. Thus we miss here the true mangroves of the genera Rhizophora, Bruguiera, Carapa, and Lumnitzera, as well as the accompanying trees and shrubs, such as Barringtonia racemosa, Excæcaria Agallocha, and Heritiera littoralis. The climbers and straggling plants that are so characteristic of the borders of the mangrove-creeks in Fiji proper are also wanting, such as Clerodendron inerme, Derris uliginosa, and Smythea pacifica; and we do not find in the Tahitian region the Giant-Sedge (Scirpodendron costatum) that is so common in the mangrove-swamps of Fiji, and occurs also in Samoa.

It is not at first sight easy to account for the absence from Tahiti of the mangrove-formation and of so many of the plants

that grow at the borders of a mangrove-swamp in Fiji. Their absence can scarcely be due to the want of suitable stations, as is indicated by the common occurrence in the Tahitian coast-marshes of Chrysodium aureum, the Great Swamp-fern, that not only abounds in the mangrove belts of Fiji, Tonga, and Samoa, but is associated with mangrove-swamps over much of the tropical zone. Nor can it be said that the currents are ineffective, or that the seeds or fruits of the missing plants possess, as a rule, insufficient floating powers. Most of the plants of the Tahitian beaches hail, like those of Fiji, from Malaya, ând have been brought through the agency of the currents ; and many of the absent littoral plants that have the same home, such as Heritiera littoralis and Clerodendron inerme, have fruits or seeds just as capable of floating unharmed over the same extent of ocean. It is not any defect in floating-power that has prevented the establishment of two such plants in the Tahitian area. Entada scandens, which in some parts of the world is a typical climber of the mangrove-formation, and in other places thrives well in the absence of mangrove-swamps, has only been recorded from Rarotonga in this region by botanists, but I believe Wyatt Gill refers to its occurrence in Mangaia in one of his books.

On the other hand, it is likely that the floating seedlings of Rhizophora and Bruguiera, which represent the only means of dispersal by the currents at the service of these mangroves, would not arrive at Tahiti in a condition favourable for the establishment of the plants. My observations, which are described in Chapter XXX., go to show that, though the seseedlings will float uninjured in still sea-water for months, they will not withstand prolonged sea-buffeting. These two genera of mangroves, it is most important to remember, supply the pioneers and the principal components of a mangrove-swamp in the Western Pacific. Where they fail to establish themselves, the requisite conditions for the large number of plants and animals that find their home in and around a mangrove-swamp would not be provided. We thus perceive that the absence from the Tahitian coast flora of several plants that are associated in Fiji with the mangrove-swamps depends on a law of association, which has already been referred to in the preceding chapter, and is not concerned with incapacity for dispersal by currents (see Note 26).

Whilst the Tahitian coast flora does not, therefore, possess the plants of the mangrove-swamp and its vicinity, it includes most of the typical beach-trees of the coral islands and reef-fronted coasts of

other parts of the South Pacific. Thus we find here on the sandy beaches Barringtonia speciosa, Calophyllum Inophyllum, Cerbera Odollam, Hernandia peltata, Guettarda speciosa, and numerous other plants that are indicated by the letter T in the list of Fijian littoral plants given in Note 2. The total number of Tahitian shore-plants is thus considerably less than that of Fiji (there are about 55 in Tahiti and about 80 in Fiji); but in its turn, as will subsequently be shown, it is much larger than that of Hawaii, where the number is about 30.

Quite three-fourths of the strand-flora of this region have buoyant seeds or seedvessels capable of floating for long periods; and there is no difficulty in assigning by far the greater share in the stocking of the beaches with their plants to the agency of the currents. The currents in their operations have indeed carried the fruits or seeds of many of these plants across the South Pacific as far as the islands extend, namely, to Ducie Island and to Easter Island. There are few more significant proofs of the efficacy of the currents in distributing plants over the Pacific than the discovery, by Mr. Arundel, of Barringtonia speciosa in Ducie Island in association with Tournefortia argentea (Challenger, Botany, III. 116).

The residue of the Tahitian coast flora possessing fruits or seeds that are unsuited for dispersal by currents includes such plants as Heliotropium anomalum, Triumfetta procumbens, Tephrosia piscatoria, Wikstrœmia fœtida, &c. The small nucules of the first-named are perhaps dispersed by granivorous birds; the fruits of Triumfetta are probably transported in birds' plumage; those of Wikstrœmia are distributed by frugivorous birds; and the seeds of Tephrosia may be dispersed like those of Heliotropium.

The recruits or intruders from the inland flora do not appear to be numerous or to give any special character to the shore flora. (See Note 27.)

From not having a personal acquaintance with this region it is not possible for me to discuss the extension of the shore-plants inland except in a general way. From the pages of the work of Drake del Castillo we can, however, infer that several plants such as Cassytha filiformis, Cerbera Odollam, Colubrina asiatica, Hernandia peltata, Morinda citrifolia, and Pandanus odoratissimus have extended inland to the mouths of the Tahitian valleys, and have ascended the lower slopes of the hills that lie near the coast. Others, like Cæsalpinia Bonduc, Gyrocarpus Jacquini, and Ochrosia parviflora, have climbed far up the mountain-sides to elevations of

from 2,000 to 2,400 feet above the sea. It is also evident from Mr. Cheeseman's memoir on the Rarotongan flora that coast plants also stray inland in that island. In an island like Rarotonga, where a sorry substitute for a mangrove-swamp exists in the form of a few coastal muddy places occupied by Vitex trifolia and Sesuvium Portulacastrum, Entada scandens takes to the hills; and thus it is that in this island it is most abundant in the interior, climbing to the tops of the highest trees and "covering acres of the forest with a dense canopy of green."

Summary of the Chapter.

(1) The Tahitian region possesses most of the plants that frequent the sandy beaches of the Pacific islands.

(2) But it lacks the mangroves and the associated plants of the mangrove-swamp.

(3) It also wants many of the plants that grow in the vicinity of such swamps.

(4) But since the plants last-mentioned often possess fruits or seeds capable of being carried great distances by the currents, their absence is to be attributed to the necessary conditions being lacking on account of the failure of the mangroves.

(5) Most of the beach plants, however, owe their existence in this region to the transport of their buoyant fruits or seeds by the currents.

(6) The negative features of the Tahitian strand-flora are mostly to be connected with the absence of Rhizophora and Bruguiera, the pioneers of the mangrove-swamp; and their absence is, in turn, to be attributed to the inability of their floating seedlings to reach this region in a fit condition for establishing themselves.

CHAPTER VII

THE HAWAIIAN STRAND-FLORA

Its poverty.—Its negative features.—Their explanation.—The subordinate part taken by the currents.—The Oregon drift.—The inland extension of the beach plants.—Summary.

COMPARED with the rich strand-flora of Fiji, that of Hawaii presents but a sorry aspect. In the number of species (30) it does not amount to half; whilst it lacks the great mangrove-formation and the luxuriant vegetation accompanying it that gives so much character to the shores and estuaries of Fiji. Strangely enough, it is also deprived of most of the familiar trees that, whether in foliage, in flower, or in fruit, form the chief attraction of the sandy beaches of the Pacific islands.

Neither the mangroves, therefore, nor the plants of the intermediate formation, are to be found in Hawaii; and when we reflect that the absentees from the beach formation include most of the trees, under the shade of which the visitor to the Pacific islands can nearly always find protection from the fierce rays of a tropical sun, it cannot be a matter of surprise that this littoral flora has such a poverty-stricken appearance. We look in vain for such shady beach trees as Barringtonia speciosa, Terminalia Katappa, and Hernandia peltata; and we are lucky if we find some small trees under which we can obtain a scanty shade.

I have been speaking, of course, of the indigenous shore-plants, those that have arrived at these islands without the assistance of man. Yet it must be added that the existing littoral flora does include some of the missing indigenous trees, though rarely in any number. There is, however, scarcely one of them that is regarded by Dr. Hillebrand as having formed part of the original flora. That botanist would indeed rob the present beach flora, scanty as it is, of most of its conspicuous plants, as far as their claims to be

considered indigenous are concerned. Dr. Hillebrand indeed includes Calophyllum Inophyllum, Hibiscus tiliaceus, Thespesia populnea, Morinda citrifolia, Cordia subcordata, and Pandanus odoratissimus in the present Hawaiian flora, and nearly all of them are to be found at times at the coast as well as inland; but he regards all, excepting the last-named, as having been introduced by the aborigines. I was not inclined at first to go quite so far as Dr. Hillebrand in this direction; but he carefully considered the case of each individual plant, and, remembering his sojourn of twenty years in the islands, his authority cannot be lightly put aside. In the list of Hawaiian strand-plants given in Note 28 there are several species not always littoral in the group, but typically littoral in other tropical regions. One species, Ipomea glaberrima, Boj., has not been recorded before from these islands.

A strong reason in favour of the contention of this botanist is that all the trees above-named are useful in some way to the natives; and, indeed, when we look at the works dealing with the floras of the islands of the South Pacific, we observe that in almost all the groups one or other of these six trees bears the reputation of having been introduced by the aborigines. All of them in their turn lose their fame as truly indigenous plants in some group or other. The occurrence of two or three useless South Pacific beach trees, that are known to be dispersed by the currents, in the indigenous strand-flora of Hawaii, would go far to invalidate Dr. Hillebrand's argument, since the six trees in dispute are also known to be dispersed by the currents. But such trees are not to be found; and we look in vain for trees like Cerbera Odollam, Guettarda speciosa, Gyrocarpus Jacquini, and Hernandia peltata, that are spread far and wide over the beaches of the South Pacific.

It is also of interest to notice how trees like Morinda citrifolia and Terminalia Katappa, concerning the non-indigenous character of which there can be but little doubt, are in our own day acquiring a littoral station. The second is not even regarded by Dr. Hillebrand as having been introduced by the natives, but is referred by him to the European epoch. After having been extensively planted, it is now, as I found, becoming a littoral tree on the coast of Oahu, and supplies its buoyant fruits in a regular way to the beach drift. Its native name of Kamani is merely that of Calophyllum Inophyllum. All the six trees in dispute are known in Hawaii by the names by which they are distinguished far and wide over the South Pacific, a fact of which the reader may satisfy himself by referring to my paper on Polynesian plant-names. The

Hawaiians, when their ancestors abode in the South Pacific, must have been well acquainted with one or other of the prevailing names of Terminalia Katappa (Talie, Tara, &c.); but it had lapsed in the memory of the race when the Europeans introduced the tree into Hawaii.

It may be added in this connection that Dr. Hillebrand weakens his argument by regarding Pandanus odoratissimus as of pre-aboriginal origin or as truly indigenous. Like the other six trees in question, its fruits are known to be capable of dispersal far and wide by the currents; and if this species of Pandanus is indigenous, we are obliged to assume that its fruits were first brought by the currents. That being so, we cannot exclude the probability of the currents having been also effective with several of the other plants regarded by Hillebrand as of aboriginal introduction, more especially those with large fruits like Calophyllum Inophyllum, and Cordia subcordata, where the alternative agency of frugivorous birds would be impracticable, at least over a wide extent of ocean. Pandanus odoratissimus is, as I venture to think, a tree that was introduced ages since by the aborigines. Next to the Coco palm, few trees have been more utilised by island-peoples, more particularly perhaps in the ruder stages of their history.

This point has been discussed at some length, because on the correctness of Dr. Hillebrand's view depends the explanation to be subsequently given of the origin of the shore-flora of Hawaii. Though differing in some details, my observations on the Hawaiian coast plants, which are given in Note 29, tend to strengthen his contention.

I now return to the consideration of some of the negative features of the Hawaiian strand-flora, and will allude first to the absence of the mangroves and of the numerous other plants that live in and around a mangrove-swamp. This cannot be connected with a total absence of suitable stations. Although it is true that there are but few large rivers and but few suitable localities, yet such localities exist. The shores of Hilo Bay might readily have been the home of a mangrove-swamp; and one can point to different places on the coast of Oahu, such, for instance, as Pearl Harbour, which in Fiji would have been occupied by a luxuriant growth of mangroves. The same argument applies to the missing beach trees, such as Barringtonia speciosa, Hernandia peltata, Guettarda speciosa, &c., that adorn the beaches of many a coral island or of many a coral-bound coast in the South Pacific.

Although in a large island like Hawaii with its lava-bound coasts but few white calcareous beaches exist where we might expect to find such a flora, yet such beaches occur wherever the scanty coral reefs are found off the coast; and it is just in those localities, as is pointed out in the account of my observations in Note 29, that the "plantes madréporiques" of the French botanists, the plants of the coral atoll and of the reef-girt coast, make their best endeavours to establish themselves. In other islands like Oahu, where coral reefs are more developed, calcareous beaches are more frequent, and there the few "madreporic" plants of Hawaii make a home.

Nor can the deficiencies in the Hawaiian strand-flora be connected with climatic conditions. That its meagre character cannot be so explained is indicated by the manner in which the Indo-Malayan shore-plants have pushed their way northward on the western side of the Pacific to the Liukiu and Bonin Islands. Here in latitude 26–27° N. we find several Fijian littoral trees and shrubs, such as Hernandia peltata, Pemphis acidula, Pongamia glabra, Sophora tomentosa, Terminalia Katappa, Tournefortia argentea, &c., that do not occur in Hawaii, although this group is some degrees nearer the equator, namely, in latitude 19–22° N. They are accompanied by the mangroves (Rhizophora, Bruguiera, &c.) in strength as far as South Liukiu in latitude 25° N.; but we learn from Dr. Warburg that the mangroves thin off further north, though they reach to South Japan, where Döderlein found in latitude 32° N. solitary examples of Rhizophora mucronata. These interesting facts of distribution, which are taken from Schimper's work on the Indo-Malayan shore-plants (pp. 85, 90), show us that we can scarcely look to climatic conditions for the explanation of the absence of mangroves and of many other tropical littoral plants from Hawaii. We form the same opinion when we regard the extension northward of the mangrove-formation on the American coasts of the North Pacific Ocean. According to the account of Dr. Seemann given in the "Botany of the Voyage of H.M.S. *Herald*," the mangroves with the coco-nut palm, and many other littoral plants common on the western shores of tropical America, reach their northern limit a little north of Mazatlan within the mouth of the Gulf of California in latitude 24° 38′ N. The parallel of 25° N. latitude, as indicated in Drude's Atlas, probably represents the extreme northern limit, which is thus five or six degrees north of the latitude of the large island of Hawaii.

Neither can the explanation be found in the deficient floating powers of the seeds or seedvessels of many of the "absentees." Those of Barringtonia speciosa, Guettarda speciosa, Heritiera littoralis, the two species of Terminalia, &c., possess great buoyant powers equal to, and probably often exceeding, those of the plants that, like Ipomea pes capræ, have succeeded in establishing themselves in Hawaii. One has only to look at the lists giving the results of flotation experiments in Notes 2 and 3, in order to realise that there are very few of the "absentee" littoral plants, the non-existence of which in Hawaii could be attributed to deficient floating powers of the fruit or seed. Being able to float unharmed for months, and in several cases even for years, the seeds or fruits of the shore-plants unrepresented on the Hawaiian beaches have been carried far and wide by the currents over the tropical Pacific even to Ducie and Easter Islands, that is, as far as the islands extend.

The only plants about which one could express a doubt concerning their ability to reach Hawaii through the agency of the currents, and to establish themselves there, are the true mangroves of the genera Rhizophora and Bruguiera. Since germination takes place on the tree, it is only through the floating seedlings that they could reach these islands; but, as shown in Chapter XXX., it is doubtful whether the seedlings would be in a fit condition for reproducing the plant after such a long oceanic voyage. If they had been as successful in establishing themselves in Hawaii as they have been in the Liukiu Islands, which lie in latitude a few degrees farther north, these two species through their reclaiming agency would alone have prepared the way for the whole mangrove formation. We have seen in the preceding chapter that the absence of the mangrove formation from Tahiti appears to be mainly due to the failure of the pioneer species of Rhizophora and Bruguiera to establish themselves there. This evidently also applies to Hawaii, the cause of their exclusion being connected neither with climate nor with station, but as in Tahiti with the general unfitness of the floating mangrove seedlings for crossing broad tracts of ocean without injury to the growing plantlet.

With regard, however, to the bulk of the "absentee" littoral plants, those of the beach-formation, no such incapacity on the part of the buoyant seed or fruit can be accepted. These plants, which have reached Tahiti in numbers, have in the mass failed to reach Hawaii. It will, therefore, be of interest to glance at the

character of the fruits of the "absentee" trees, which a traveller fresh from a visit to the coral islands and reef-girt coasts of the South Pacific sadly misses on the Hawaiian beaches. We notice in the first place that the absent trees, such as Barringtonia speciosa, Cerbera Odollam, Guettarda speciosa, Heritiera littoralis, Terminalia Katappa, &c., have large fruits which could only have been carried to Hawaii by the currents, the agency of birds being quite out of the question. On the other hand, almost all the littoral plants of Hawaii, whether trees, shrubs, or herbs, which are regarded as truly indigenous by Mann, Hillebrand, and other Hawaiian botanists, have only small fruits or seeds available for dispersal, from which the agency of birds cannot, on the point of size, be excluded. Amongst these shore plants possessing buoyant seeds or fruits are Cassytha filiformis, Colubrina asiatica, Ipomea pes capræ, Scævola Kœnigii, Vigna lutea, and Vitex trifolia; whilst amongst the plants with non-buoyant fruits or seeds are to be reckoned Heliotropium anomalum, H. curassavicum, Tephrosia piscatoria, Tribulus cistoides, &c. The seeds or seedvessels of the plants of the buoyant group possess great floating powers; and it seems at first sight scarcely credible that the currents which have failed to establish Barringtonia speciosa, Guettarda speciosa, and the other trees that through this agency have often found a home on the remotest islands of the Pacific, should have succeeded in the instances of plants like Scævola Kœnigii and Vitex trifolia.

It would indeed almost seem that in nearly all cases where it would be impossible in point of size for a bird to transport the fruit or seed of a shore-plant to Hawaii, such a plant is not to be found in the strand-flora of that group, even though it is well adapted for dispersal by the currents. Many of the littoral trees missing from the Hawaiian coast-flora, having large buoyant fruits, come into this category; and grave suspicion is thus apparently cast on the agency of the currents in the case of the plants with small fruits and seeds that really compose the strand-flora, even when their capacity for sea-transport has been well established by observation and experiment. The efficacy of the currents would thus seem to be called into question for the whole littoral flora of Hawaii.

If, however, we were to adopt such a sweeping conclusion we should be led into an error. It is pointed out in the following chapter that nearly all these large-fruited beach trees that are found far and wide over the South Pacific, but are absent from Hawaii, do not occur as indigenous plants in America. If, there-

fore, the fruits of such Old World littoral trees as Barringtonia speciosa, Cerbera Odollam, Guettarda speciosa, Ochrosia parviflora, Terminalia Katappa, &c., that could be dispersed only by the currents, have failed to reach Hawaii, it is essential to remember that they have also failed to reach America. This suggests that Hawaii may have received some of its littoral plants from America through the agency of the currents; and it is shown in the following chapter that, as a rule, when a South Pacific plant with buoyant fruits or seeds is not found in America, it is equally absent from Hawaii. The question thus acquires quite a different aspect, and we shall accordingly have to regard tropical America in the next chapter as a possible centre of diffusion of littoral plants over the globe, a centre possibly as important as that connected with the tropics of the Old World.

Although, however, the currents have played a part in stocking the Hawaiian beaches with their plants, their share in the work has been unimportant, and the number of plants concerned is limited. If we take away the seven or eight littoral plants introduced by the aborigines, as well as the three endemic species as indicated in the list in Note 28, and then remove from the residue the plants with small fruits or seeds possessing little or no buoyancy, there remain only the following eight species, the presence of which in Hawaii might be attributed to the currents, namely, Cæsalpinia Bonducella, Cassytha filiformis, Colubrina asiatica, Ipomea glaberrima, Ipomea pes capræ, Scævola Kœnigii, Vigna lutea, and Vitex trifolia. Of these plants, three species, those of Cassytha, Scævola, and Vitex, possess fruits that would be likely to attract frugivorous birds, and are in some cases known to be dispersed by them (see Chapter XIII.); so that we are not in these instances restricted to the agency of the currents. With the other five the currents offer the readiest explanation, but, as is indicated in the cases of Cæsalpinia Bonducella and Ipomea glaberrima (Chapter XVII.), it is quite possible that birds have occasionally intervened. Altogether we may infer that in stocking the Hawaiian beaches with their littoral plants the currents have taken a subordinate part.

Coming to the Hawaiian littoral plants having seeds or fruits that have no floating power, we find that they present a motley group. It has been already remarked that this is the group of shore plants that derives most recruits from the inland flora, and that it is in this group that the differences between the shore-floras of tropical regions find their expression. Yet a very odd collection of plants is here exhibited. Sometimes the beach-flora is composed

in great part of these plants; and a sorry spectacle is presented by a beach possessing such plants as Gossypium tomentosum, Heliotropium anomalum and H. curassavicum, Lipochæta integrifolia, Tephrosia piscatoria, Tribulus cistoides, &c. Yet to the student of plant-distribution such a motley collection would be full of suggestiveness. From the circumstance that species of Cuscuta, Jacquemontia, and Lipochæta, that are peculiar to the Hawaiian Islands, have made their homes on the beach, he would infer that since Nature has been compelled to borrow from the endemic inland flora, there has been some difficulty in stocking the beaches with their plants. The occurrence of endemic species amongst the strand-plants would be viewed by him as especially indicating incapacity on the part of the ocean currents.

Yet in the quantities of drift timber, showing evidence of many months and probably even of years of ocean-transport, to be seen stranded on the weather coasts of these islands, the observer discerns undoubted evidence of the efficacy of the ocean currents. But what he finds are huge stranded pine logs of "red-cedar" and "white-cedar" from the north-west coasts of America. He may search the drift for days together, as I have done, and discover no tropical fruits or seeds except such as could be supplied by the present Hawaiian flora. The subject of this drift is especially discussed in Note 30; and it need only be mentioned here that it is not improbable that, as shown in the next chapter, some drift may reach Hawaii from tropical America under exceptional conditions, and that its presence is masked by the Oregon drift.

The agency of the drifting log in carrying small seeds in its crevices would be effectual in the instance of plants from the temperate coasts of North America. For example, the nutlets of Heliotropium curassavicum, which have no buoyancy, might easily be washed, together with sand, into the cracks of a pine log stranded temporarily on the Oregon coast where this plant occurs. The *modus operandi* was brought home to me when examining the drift brought down by the Chancay River on the coast of Peru. Here I found this species of Heliotropium growing on the margin of a swamp near some stranded logs, that would probably be carried out to sea when the river was next in flood.

It is probable, I may add, that the seeds or fruits of some of the plants of the non-buoyant group of the Hawaiian littoral flora may be dispersed in birds' plumage. For instance, the spiny fruits of Tribulus cistoides sink in sea-water; but they are well suited for entangling themselves in birds' feathers.

It is possible that the hairy seeds of Gossypium tomentosum may have been thus distributed; but there is much that is enigmatical about this plant (see Chapter XXVI).

THE INLAND EXTENSION OF THE BEACH PLANTS OF HAWAII.—When we regard the inland extension of littoral plants in Hawaii, we get fresh indications of the meagreness of the strand-flora. Several of the species, as Cæsalpinia Bonducella, Cassytha filiformis, Tephrosia piscatoria, &c., show themselves only occasionally on the sandy beaches, though they are common enough on the old scantily vegetated lava-flows near the coast and are often found miles inland. Indeed, Dr. Hillebrand not infrequently in describing the station only gives prominence to the situation of the plants away from the beaches, and places most of them on the old lava plains that extend inland from the coast. It is only by a detailed examination of extensive coast lines in these islands that I have succeeded in preserving to a small degree their reputation as beach plants. A few of them behave somewhat strangely in their inland station. Thus, the seeds of Cæsalpinia Bonducella obtained from various localities showed no buoyancy in my experiments; and had I not found a solitary buoyant seed in the stranded drift I should have inferred that this was a rule without exception.

It is to be remarked that whilst some plants like Scævola Koenigii occasionally stray a few hundred yards inland on the surface of the old lava-flows, others like Ipomea pes capræ and Vitex trifolia, that are spread far and wide over the inland plains of Fiji, are confined in Hawaii to the beaches and their immediate vicinity. Some of the plants like Hibiscus tiliaceus, Morinda citrifolia, and Pandanus odoratissimus, that are regarded as having been introduced by the aborigines, behave exactly like indigenous plants in the inland plains; but this is not necessarily an indication of an indigenous plant in this group, since the Cactus (Opuntia Tuna) and the Castor-Oil Plant (Ricinus communis) have spread all over the drier lower regions of the islands, whilst Aleurites moluccana, the Candle-Nut Tree, which has no means of reaching these islands without man's agency, now forms entire woods on the mountain slopes, usurping the place often of the original forests. . . . Further details relating to this subject are given in Note 31.

The principal points in the foregoing discussion of the strand-flora of Hawaii may be thus summed up:—

(1) The indigenous, that is, the pre-aboriginal, strand-flora of this group lacks not only the mangroves and their associated plants, but also most of the characteristic beach-trees of the South

Pacific, which are known to owe their wide distribution in tropical regions to the currents.

(2) The meagreness of the littoral flora is intensified by the tendency of some of the plants to extend inland and to desert the coasts, and by the occurrence on the beaches of peculiar species not found outside the Hawaiian Islands.

(3) The absence of the mangrove formation and of so many of the typical beach trees of the Pacific cannot be attributed either to the lack of suitable stations, or to climatic conditions, or to deficient floating power of the seed or fruit.

(4) As in the case of Tahiti, the mangroves and their associated plants are lacking because the floating seedlings of Rhizophora and Bruguiera, the pioneer plants of a mangrove-swamp, have failed to reach Hawaii in a fit condition for establishing themselves. The numerous plants that accompany a mangrove-swamp have thus been unable to find a home, though the buoyant powers of their fruits or seeds are often great.

(5) With the missing beach-trees, however, which possess fruits that can float for years unharmed in sea-water, no such incapacity is suggested. Most of them have large fruits, which could only reach Hawaii through the currents. This absence from the Hawaiian indigenous strand-plants of most, if not all, of the large-fruited species, where on account of size the agency of birds is absolutely excluded, is very remarkable; and it at first seems to throw grave suspicion on the efficacy of the currents for the whole strand-flora.

(6) It is, however, to be noticed that these large-fruited beach trees have not only failed to reach Hawaii but have also failed to reach America. The question thus acquires quite a different aspect, and America becomes the possible source of most of the Hawaiian plants with buoyant seeds or fruits.

(7) This subject is discussed in the next chapter; but it is here shown that at their best the currents have taken but a secondary part in stocking the Hawaiian beaches with their plants, since many of the plants have non-buoyant seeds or fruits.

(8) The drift stranded on the shores of the Hawaiian Islands is composed of logs from the north-west coast of North America. No drift from the south has been discovered; but it is not unlikely that future investigators will find some seed-drift from tropical America.

CHAPTER VIII

THE LITTORAL PLANTS AND THE CURRENTS OF THE PACIFIC

The working value of the currents as plant-dispersers.—The relation between the currents and the distribution of shore-plants.—The clue afforded by the American plants.—Two regions of tropical shore-plants, the American and the Asiatic.—America, the home of the cosmopolitan tropical shore-plants that are dispersed by the currents.—Hawaii and the currents.—Summary.

ACTIVE as the currents are in dispersing seeds and fruits over the Pacific, it should be remembered that those plants that owe their distribution to this agency are only shore-plants, and not, indeed. all the shore-plants, but only those with buoyant seeds or fruits. Even the coral atoll owes a great deal to the agency of the fruit-pigeon and of other birds; for instance, their species of Ficus, Eugenia, and Pisonia. In order, therefore, not to form an exaggerated notion of the efficacy of the currents, it will be necessary to obtain some numerical idea of what they have really accomplished in transporting seeds and seedvessels over the oceans in a state fit for successful germination on the shores upon which they are stranded. It is requisite to make this proviso, because in some cases the currents work to no purpose. Thus, the empty nuts of Aleurites moluccana are carried far and wide over the Indian and Pacific Oceans, and are stranded on the beaches of the various islands, as I have found myself in the cases of Keeling Atoll, Java, and Fiji. The Coco-de-Mer, or the Double Coco-nut Palm, is another apt instance. Though its fruits have been carried far and wide over the Indian Ocean, the species is restricted to the Seychelles. So also the acorns of various species of Quercus are widely but ineffectually distributed by the currents both in temperate and tropical regions. (This subject of useless dispersal is dealt with in Chapter XIII.)

It is essential to bear in mind at the outset that for their inland plants the Pacific islands can draw on the floras of a relatively large portion of the globe. Such plants, having as a rule fruits or seeds that sink in sea-water, or are incapable of floating for long periods, could only have arrived at these islands, where man's interference is excluded, through the agencies of winds and birds, assisted by other lesser agencies, as those of bats, insects, &c. On the other hand, for their littoral plants, which are for the most part dispersed by the currents, the source of supply is very restricted. The shore-plants with buoyant seeds or fruits of the islands of the tropical Pacific, that are here dealt with, number only about seventy, and it is not likely that this number will be greatly increased, since, whatever may be the deficiencies in our acquaintance with the inland floras of these islands, we have a fairly complete knowledge of the strictly littoral plants.

I do not suppose, indeed, that the number of such plants with seeds or fruits capable of being transported unharmed over wide tracts of sea would much exceed 100 for the whole Indo-Pacific region from India to Tahiti. Professor Schimper gives a list containing 117 tropical plants distributed far and wide over the shores of this region, and made up of species dispersed by currents, birds, and man. Taking a liberal estimate, not over two-thirds of the plants mentioned in this list are dispersed by currents. Then, again, if the flora of a coral atoll, like that of Diego Garcia or of the Keeling Islands, is taken as affording an index of the work of the currents, the number of plants dispersed by the currents would appear to be indeed restricted, since in either case their indigenous flowering plants, including those of both the buoyant and non-buoyant groups, do not exceed fifty.

About twenty years ago, Mr. Hemsley, who, in his work on the botany of the *Challenger* Expedition, prepared the way for the investigation of this subject, made a list of not less than 120 plants, almost all tropical, that are "certainly or probably dispersed" by the currents (Introd. *Chall.* Bot., p. 42). This is admittedly only a preliminary list, and as the result of recent investigations some plants have to be omitted and others to be added; but I doubt whether, numerically, it is far below the mark. The relative efficacy of the currents seems to have been first systematically discussed by De Candolle in his *Géographie Botanique*, which was published in 1855. Data were then very scanty, and out of a list of nearly 100 inter-tropical species (Old World plants found in the New World and New World plants found in the Old World)

he designates nine only as exclusively dispersed by the currents. Even this list, in one respect, needs correction (see Note 33); but it is of interest to note that this eminent botanist from the first never looked upon the agency of the currents as a very important factor in plant-dispersal; and, finding in the specially directed and carefully performed experiments of Thuret confirmation of his views, he reiterated his opinion in a note to that author's paper in 1873 (cited in Chapter III.).

However, De Candolle was quite right in minimising the effect of currents on the distribution of plants. His extensive survey of the plant-world from the standpoint of dispersal gave him that sense of proportion in assigning values to dispersing agents which enabled him to feel his way almost intuitively, even where exact data were often lacking. It is, however, a little disappointing to find such a slight treatment of the subject in Kerner's great work on the Natural History of Plants, though one can scarcely controvert his opinion that the dispersion of plants, as a whole, is not appreciably affected by this process. Numerically speaking, this is in the main correct; yet it is here that the genius of Schimper led him to recognise and to mark out a line of investigation, fruitful in important results, in connection with the weighty question of "Adaptation." If the author of this work has been able to add a little to our acquaintance with this subject, he owes much to the inspiration he received from Schimper's memoir on the Indo-Malayan Strand-Flora.

Still, it must be admitted that the effectual operations of the currents as plant-dispersers are limited to the shore-plants with buoyant seeds or fruits. If we were to include in our list the shore-plants of temperate regions that possess seeds or fruits capable of floating in sea-water for long periods, and of afterwards germinating, the total for the whole world would not, I imagine, reach 200. We cannot here concern ourselves with those purely river-side plants that contribute their buoyant seeds and seed-vessels to river-drift, since there is no evidence indicating that river-side plants are effectively dispersed by the currents unless they also frequent the estuary and the coast-swamp; and in that case they come under the head of littoral plants. The total for the whole British flora would probably not far exceed a dozen, and nearly all of them are very widely dispersed.

The working value of the currents as plant-dispersers in the Pacific can be rudely estimated by the number of littoral plants with buoyant seeds or fruits that occur in the various groups.

Most of these plants hail from the Indo-Malayan region. Speaking generally of the extension eastward of the Indo-Malayan strand-plants over the Pacific, Prof. Schimper (page 195) remarks that they become fewer and fewer in number as they extend farther from their original home, their number shrinking to a very few in the most remote groups of the Marquesas and the Hawaiian Islands. This is well illustrated in the following numerical results that I have prepared. Of the whole number, some seventy in all, of the littoral plants of the tropical Pacific with buoyant seeds or fruits, Fiji possesses about sixty-five, Tahiti about forty, and Hawaii only about sixteen. As shown, however, in Chapter VII., some of the Hawaiian littoral trees that are useful to the aborigines were probably introduced by them. The number actually introduced through the currents into Hawaii in all likelihood therefore does not exceed ten. There is a method in this diminution in numbers, as the plants migrate eastward and northward over the Pacific, which has been described in detail in the preceding chapter. The efficacy of the currents as plant-dispersers in the tropical Pacific therefore diminishes as we proceed eastward.

In the South Pacific the littoral plants preserve their Old World origin as far as the Polynesian archipelagoes extend eastward across to Pitcairn, Elizabeth, and Ducie Islands, where we find in one or other of them such characteristic Indo-Malayan beach trees as Barringtonia speciosa, Cerbera Odollam, Guettarda speciosa, Hernandia peltata, and Tournefortia argentea (see Note 34). In the more distant Easter Island there is a suspicion, for the first time, of immigration from South America in the presence of Sophora tetraptera. In the islands relatively close to the American continent, as in Juan Fernandez and in the Galapagos group, the Indo-Malayan strand-plants are no longer represented.

We come now to consider the relation between the distribution of the shore-plants and the currents. It is quite legitimate to discuss the currents of the Pacific from the botanist's point of view, that is to say, from the standpoint of the distribution of littoral plants with buoyant seeds or fruits. For ages the buoyant seeds and fruits of the strand-plants of the tropical Pacific have been drifting over that ocean, and we have the results now before us in the dispersal of the species to which they belong. There is no necessity to endeavour to make the distribution of such littoral plants square with the arrangement of the currents as shown in a chart. The usual result of such a comparison has been to lead the

investigator, whether an anthropologist, a zoologist, or a botanist, to find his facts at variance with the course of the prevailing currents. Man, animals, and plants have entered the Pacific from the west, whilst the most available currents are from the east; and one may be perhaps permitted the solecism that the Pacific islands have apparently been stocked with their shore-plants, with their aborigines, and with much of their fauna by currents running in the wrong direction. These Pacific islands could only have had a direct communication with the Old World, from which they have mainly derived their shore-plants, by the currents; but since both the aborigines and the plants have forced their way across the ocean to the Tahitian region in the teeth of the regular currents, indicated as such in the chart, we are compelled to assume that they have availed themselves either of the Equatorial Counter-Current or of the occasional easterly drift currents that mark the prevalence of westerly winds during the short season of the year when the easterly trade-winds do not prevail.

The Equatorial Counter-Current hypothesis would involve a preliminary crossing of the whole breadth of the Pacific Ocean, that is to say, a voyage of some 8,000 miles, before the drifting seed doubled back to the Polynesian Islands. The other view is a much more probable one, as is sufficiently indicated by the following extract from the "Admiralty Sailing Directions for the Pacific Islands" (II., p. 25, 1900) . . . "In the western part of the Pacific these trades . . . are frequently interrupted by winds which blow from west or north-west, especially during the months of January, February, and March, when the north-west monsoon of the Indian Ocean extends out in the Pacific as far as the Samoa Islands." In various works on this region one may find reference to canoes blown off the shore during this season and carried some hundreds of miles to the eastward. A ship can then sometimes sail with a fair wind from the southern end of the Solomon Group to the Fijis; and as we learn from Mariner, the crocodile may be at such times carried away from the Solomon Islands and stranded in Fiji. Mr. Hedley, in his exceedingly interesting paper on a zoo-geographic scheme for the mid-Pacific (*Proc. Linn. Soc. N.S.W.*, 1899), gives many details of this nature; but there is no space to deal further with the matter here.

After all, the botanist must take his cue from the drifting seed and the distribution of the plant. He finds the seed floating in the open sea as well as stranded on the beach. He then discovers the plant growing on the beaches, and by experiment he tests the

floating capacity of the fruit or seed. Finally he ascertains the home of the plant. He does this for all the littoral plants with buoyant seeds or fruits, and he forms his own conclusions of the efficacy of the currents independently of the current-chart, remembering that he has in Time an important factor that the geographer does not possess in dealing with the currents. The effect of time has often been to obscure the differential results of the operations of the currents in the case of those species that, like Barringtonia speciosa, are almost universally distributed in the islands of the Pacific. It is obvious that such plants cannot aid us much in the matter of ascertaining the track followed by the drifting seed in entering this ocean. But if we find a littoral plant with buoyant seed or fruit that has only partially performed the traverse we shall possess in the interrupted operation an important piece of evidence.

Several years ago, in my paper on Polynesian plant-names, read before the Victoria Institute, I developed this argument when endeavouring to find in the floating seed a clue to the route pursued by the Polynesians in entering the Pacific. Since that time my acquaintance with these islands and their plants has been considerably extended; but no important modification of the principal argument is now needed. It was then pointed out that in Nipa fruticans, the swamp-palm of the Malayan Islands and of tropical south-eastern Asia, we have a plant well fitted for the purpose and one well known to be dispersed by the currents over small tracts of ocean. The Nipa Palm has attempted to enter Polynesia from the Malayan region by two routes, namely, by Melanesia and by Micronesia. Along the first route it has in the course of ages reached the Solomon Islands, where I found it in 1884. Along the second route it has extended its range to Ualan at the eastern end of the Caroline Group, where it was observed by Kittlitz many years ago, as indicated in the narrative of his voyage (*Reise nach russische America, nach Mikronesien*, etc., 1858, ii. 35), and in Dr. Seemann's English edition of the same author's *Vierundzwanzig Vegetationsansichten . . . . des stillen Oceans.*

The question now arises as to which of these two routes was taken by the drifting seed. In my paper I adopted the view that the shore plants reached Fiji and Samoa by Micronesia, that is to say, by the Caroline, Marshall, and Gilbert Groups. This is the route which, as mentioned by Mr. Hedley in the paper above quoted, Mr. Woodford prefers for some of the Lepidoptera; and it is the one that is favoured by Mr. Wiglesworth for the birds, since


TRADE ROUTES
OF THE
PACIFIC OCEAN
(On Mercator's projection)
Steamer Routes .... Telegraph Cables ——
Distances are given in Nautical Miles
DOMINION OF CANADA
NORTH AMERICA
UNITED STATES
MEXICO
SOUTH AMERICA
CHINA
JAPAN
MANCHURIA
KOREA
AUSTRALIA
NEW ZEALAND
OCEANIA
EAST INDIAN ARCHIPELAGO
PHILIPPINE ISLANDS
Vladivostock to Victoria 4800 m.
Yokohama to Victoria 4320 m.
Yokohama to S. Francisco 4750 miles
Yokohama to Honolulu 3445 m.
San Francisco to New York sailing
Panama Route
Tropic of Cancer
Equator
Tropic of Capricorn
Long. E. of Green.
Long. W. of Green.
John Bartholomew & Co. Edin.

in his memoir entitled *Aves Polynesiæ* he remarks that certain indications tend to show that the Pelew Islands have served as a sort of bridge for the spread of species from Indo-Austro-Malaya right across the Pacific. Though I still think that the beach trees, most of which would find a home on the numerous coral atolls of the Marshall, Gilbert, and Ellice Groups, often followed that track, yet I am now inclined to consider that the mangroves and their associates, plants which find their most suitable home in the estuaries of large elevated islands, like those of the Solomon Group, in all probability reached Fiji in the mass by the Melanesian route.

Although the Old World has supplied to the Pacific islands most of their littoral plants that are dispersed by the currents, that is to say, the plants with buoyant seeds or seed vessels, yet there is an appreciable American element, and it is with the plants occurring in the New World that we are now concerned. The total number of the littoral plants of these islands that possess buoyant seeds or fruits is, according to the lists given under Note 35, about seventy. Of these about forty-five are exclusively Old World species, sixteen occur in both the Old and New Worlds, three are exclusively American, and six are Polynesian.

The question we have now to ask ourselves is whether the shore plants common to both the Old World and America have their homes in America, or whether they have been derived from the other hemisphere. With one or two exceptions, as in the cases of the Australian genera Dodonæa, Scævola, and Cassytha, which, as shown in a later page in this chapter, present no great difficulty, there does not seem to be any serious objection, as far as the numerical distribution of the species is concerned, in regarding America as a possible home of the genus. It is not often we shall come upon such a striking instance of the principle that where the species are most numerous there is the home of the genus, as in the instance of Cocos. The Coco-nut palm has been carried around the world through the agencies of man and the currents, whilst the home of the genus is in America.

Now assuming that in having to choose between the Old World and the New World as the home of most of the genera in the list we selected the latter, we have to ask ourselves in what degree this would be consistent with the place America holds with regard to the distribution of tropical shore-plants dispersed by the currents and with reference to the arrangement of the currents. If we except the African continent, there is no part of the world that

bears such a definite relation to the currents as America, and with an ordinary chart of these regions their arrangement is to be understood at a glance. Yet strange to say, as far as the distribution of tropical littoral plants is concerned, America holds a position that the present system of the currents on its coasts will not altogether explain. Within the lifetime of the species of mangroves and other plants of the coast swamps that are found on both the Pacific and Atlantic coasts of tropical America the two continents of this name have been united by the emergence of the Isthmus of Panama.

Few things are more significant in plant-distribution than the arrangement of the tropical littoral plants with buoyant seeds or fruits, a subject that is discussed with some detail by Professor Schimper in his work on the Indo-Malayan strand-flora (page 190). These plants group themselves into four sections :—

(*a*) Those of the Pacific and Atlantic coasts of tropical America (including the West Indies) and of the West Coast of Africa. They include mostly plants of the mangrove-swamps and their vicinity, such as Anona paludosa, Avicennia tomentosa, A. nitida, Conocarpus erecta, Laguncularia racemosa, Rhizophora mangle, etc.

(*b*) Those of the Old World excluding the African West Coast and extending from the East Coast of Africa eastward to the Pacific islands. This is much the largest group and comprises many of the plants named in the list given in Note 35 under Old World species. One may cite as examples of plants ranging almost all over this area, Barringtonia speciosa, B. racemosa, Bruguiera gymnorhiza (in its most comprehensive sense), Carapa moluccensis, Derris uliginosa, Guettarda speciosa, Hernandia peltata, Heritiera littoralis, Pemphis acidula, Rhizophora mucronata, etc. Plants of the mangrove-swamp and of the beach are, therefore, here included.

(*c*) Those occurring all around the tropics and including many of the plants mentioned under Note 35 as Pacific island shore-plants found also in America. Most of them belong to the Leguminosæ, and there may here be mentioned Canavalia obtusifolia, Cæsalpinia Bonducella, Entada scandens, Gyrocarpus jacquini, Ipomea pes capræ, Sophora tomentosa, and Vigna lutea.

(*d*) Those confined to a portion of the two great regions, such as Nipa fruticans in the Old World, and the Manchineel (Hippomanes mancinella) to tropical America.

It is to be noted that the ubiquitous species do not include any

of the mangroves. Each of the two regions has its own species, none being common to both the American and Asiatic regions, although, as is shown in Chapter XXX., the American species of Rhizophora is now seemingly breaking its bounds and intruding into the Pacific islands. On the other hand, some of the mangrove genera, Avicennia, Carapa, and Rhizophora, are found all round the globe, whilst others are restricted to one or other of the two regions, Bruguiera, Lumnitzera, and Sonneratia, for instance, to the Old World region, and Laguncularia to the American and West African region.

For convenience we may designate the two great regions of tropical strand-plants, with buoyant seeds or fruits, the American and the Asiatic regions, remembering that the first includes both coasts of America as well as the African West Coast, whilst the second extends from the East Coast of Africa to Polynesia. Excluding the ubiquitous species, these two regions are well distinguished from each other. If we look at the chart of the currents we perceive the reason of the American region including the West African Coast, and we see why none of the indigenous plants of this region occur on the African East Coast. So also with the Asiatic region, a glance at the chart will show that all the portions of its area are in connection with each other directly or indirectly through the currents, and that only time is required for the transport of buoyant seeds over most of the region.

Hitherto I have mainly followed Professor Schimper in this matter ; but since my visit to Ecuador and the Panama Isthmus some further considerations have presented themselves to me. If the reader will look again at the map of the currents, he will observe that there is little reason for supposing that the Asiatic region can lend its littoral plants to the American region. On the other hand there are greater facilities, as far as currents are concerned, for America supplying the Asiatic region, namely by means of the great equatorial currents that course westward across the Pacific to the tropics of the Old World.

It would therefore seem that the American region can receive nothing by the currents from the Asiatic region. If accordingly it gives but gets nothing back, we are compelled to assign an origin in the American region to all littoral plants dispersed by the currents that are found in the tropics around the globe. This is what we have already regarded on other grounds as possible for nearly all the littoral plants of the tropical Pacific with buoyant seeds or seedvessels that are found in America. These plants are

practically the same as those distributed around the tropical zone which are enumerated in the list given under Note 35, *b*. With their home in America, by crossing the Pacific they would ultimately arrive at the East African coast, where their course westward would terminate; whilst commencing their journey from the east side of the American continent they would reach the West African coast; and their distribution around the tropics of the world would be explained. There follow from these considerations the corollaries that a tropical strand-plant dispersed by the currents which has its birthplace in Asia could never reach the American region, and that American strand-plants are for the most part native-born, excepting those, if there are any, that hail originally from the African West Coast.

It is necessary in passing to explain the similarity of shore plants on the Pacific and Atlantic coasts of Tropical America. For the mangroves and their accompanying plants inter-communication between the two coasts is now impossible; and a communication between the two oceans must be postulated within the lives of the existing species. For the plants like Entada scandens and Ipomea pes capræ, which occur inland as well as at the coast, it is easy to show that in the case of the Panama Isthmus, their seeds could be readily carried into the Atlantic and Pacific Oceans by rivers draining the opposite slopes of the same "divide," so that the dispersal of the same species from a common centre into two oceans may be seen in operation in our own day. My observations on this subject are given in Chapter XXXII., to which the reader is referred.

I have now gone far enough to indicate the place that America holds with regard to the distribution of tropical shore-plants dispersed by the currents and with regard to the currents. There is every probability, as I venture to think I have shown, that the Pacific islands have derived most of their ubiquitous shore-plants with buoyant seeds or fruits from America. But one of the results of our discussion of America in this double aspect was that excepting in the case of the African West Coast it gives but does not receive plants from the Old World. We apply this test, with perhaps a little hesitation, to the shore-plants of the Pacific islands that are dispersed by the currents; and we find, as will be seen below, that it is responded to in a remarkable manner.

It has been observed in the previous chapter that scarcely any of the large-fruited beach-plants of the South Pacific islands, that could only have been dispersed by the currents, have reached

Hawaii. We do not find amongst the truly indigenous coast flora of this group any of the following trees: Barringtonia speciosa, Calophyllum Inophyllum, Cerbera Odollam, Guettarda speciosa, Hernandia peltata, Ochrosia parviflora, Pongamia glabra, Terminalia Katappa, Terminalia littoralis, &c. It was also noted that the currents had not only failed to establish these plants in Hawaii, but that they had also failed to establish them in America, the suggestion being that the Hawaiian Islands had been, in part at least, stocked by the currents from America. That the Indo-Malayan strand-plants in their extension eastward over the Pacific should have failed to reach America, is a result we might have expected from the arrangement of the currents. Yet mingled with them we have plants like Ipomea pes capræ, Canavalia obtusifolia, and Sophora tomentosa, that also occur in America. Since, however, their seeds are not better adapted for accomplishing the passage across the Pacific from the Old World to America than the equally buoyant fruits of the above-named littoral trees that have failed, the presumption arises that their home is in America, and that they have performed the easier passage across the Pacific westward from America to the Old World.

The exclusion of so many characteristic shore-trees from America that range often over the whole tropical region from the African East Coast to the islands of the Central Pacific, is not a matter of seed or fruit-buoyancy, but a matter concerned with the home of the species, and with the arrangement of the currents. Those shore-plants of this region that occur also in America have their home in that continent, and have subsequently been carried across the Pacific by the currents westward to the Asiatic shores.

The only exceptions, that I can recall, to the rule that America does not receive shore-plants dispersed by the currents from the Old World, are presented by the three Australian genera, Dodonæa, Scævola, and Cassytha, of which widely spread littoral species occur in America, namely, Scævola Lobelia, Dodonæa viscosa, and Cassytha filiformis. They offer, however, but little difficulty, since, as pointed out in other parts of this work, Dodonæa viscosa has probably been in part dispersed by man, whilst the other two species are as well fitted for dispersal by birds as by currents. The occurrence therefore of these species in America does not necessarily raise the question of the currents.

The same exclusive principle is illustrated in the scanty littoral flora of Hawaii. Deprived, like America, of the characteristic large-fruited beach-trees of the South Pacific, species that could

only have reached it through the agency of the currents, it is scarcely to be expected that it would have received its few littoral plants with buoyant seeds from the source which has failed it in the cases of the numerous absentees. It is to America therefore that we look for the source of its littoral plants as far as the agency of the currents is concerned.

The Hawaiian Islands contain about twelve plants, named in the list given in Note 36, that possess seeds or fruits known to be dispersed by the currents, and capable, as experiments indicate, of floating in sea-water for prolonged periods. Not all of them are at present littoral in their station in this group ; but their claim to be considered such in other regions is established in the Note above mentioned. Of these plants, seven at least are found in America, five in the Old World also, and two exclusively in America. This proportion of American plants is far greater than that characterising the whole littoral flora of the Pacific islands dispersed by currents, where out of some seventy species only nineteen are found in America (see Note 35). As far as the distribution of the plants is concerned, it is therefore quite possible that Hawaii has received most of its plants that are dispersed by the currents from tropical America.

We will now consider how such a possibility is in accordance with the arrangement of the currents in the North Pacific. If we look at the Quarterly Current Charts for this ocean published by the British Admiralty we notice that all through the year the Hawaiian Group lies more or less within the area of currents flowing from the West Coast of America, the Northern Equatorial Currents as they are collectively named. Except in the winter months these currents come from the N.E. and E.N.E., and bring drift from the coasts of British Columbia, Oregon, and Northern California. It is then that they pile up huge pine logs on the shores of the Hawaiian Islands, as I have described in Chapter VII. and in Note 30; and, according to Dr. Hillebrand, they transport this drift timber much farther south to the shores of the Marshall and Caroline Groups. One might cite other facts illustrative of the working of these currents, such as one finds in the pages of Fornander and other authors; but this would scarcely come within the province of this work. I may here remark that when in Honolulu I was informed that a bell-buoy which had got adrift on the Californian coast was subsequently washed up on the coasts of Kauai. It is stated in Findlay's "North Pacific Directory" (1886, p. 1068), that a junk carrying nine hands that had been

blown off the south coast of Japan in a typhoon, anchored, after ten or eleven months at sea, in December, 1832, near Waialea in Oahu, the view taken of its course being that after drifting along in the Japan Current it came within the range of the south-west current that carries pine timber to Hawaii from the West Coast of America.

The portion of the Northern Equatorial Current that strikes the Hawaiian Group during the greater part of the year is no doubt a south-westerly deflection of the Japan Current from the American West Coast; and it would be impossible to find any tropical drift mingled with the pine logs stranded on the islands during that period. However, in the winter months, centering in January, the Japan Current flows down the West Coast of America to about the latitude of Cape Corrientes on the coast of Mexico, before being deflected westward. Here it meets with a portion of the Peruvian Current, and both flow westward, the united stream striking probably only the southernmost islands of the Hawaiian Group. It is at this season alone that there would be any likelihood of drift from tropical America being stranded on the Hawaiian beaches, and it is quite possible that at such a time the Northern Equatorial Current may carry intermingled in its stream pine logs from Oregon and seed-drift from Panama.

I am not inclined to attach any value except in the Western Pacific to the agency of the Equatorial Counter-Current in transporting seeds and fruits over the Pacific. It presents seemingly the only opportunity of the transportal of the seeds and fruits of Asiatic littoral plants to America; but if at all effective in this way, it would have endowed the littoral flora of the western shores of tropical America with many of the trees so characteristic of the coral islands of the Pacific. In this sense, it has failed completely as an effective agency in plant-dispersal; and judging by results we may, I think, dismiss it from our consideration. However, Dr. Hillebrand (p. xv.) assumes that during the prevalence of south-westerly gales in winter in the Hawaiian Islands, the Equatorial Counter-Currrent would be pushed northward so as to mingle to the east of the group with the North Equatorial Current. In this manner it is supposed that seed-drift brought direct from the Asiatic side of the Pacific would be stranded on these islands. This appears to me to be most improbable, since some ten or twelve degrees of latitude usually intervene between the Hawaiian Group and the Equatorial Counter-Current (*see* Admiralty Sailing Directions, Pacific Islands, 1900, II., 31, and the

Quarterly Current Charts; also Encyclopædia Britannica, vol. 18, p. 118).

The most serious objection from the botanist's standpoint against such a view as that of Dr. Hillebrand is the absence from Hawaii of most of the shore-plants that we should expect the currents to have brought from the Old World. It is also evident that as far as the currents are concerned the Hawaiian Islands are far more likely to receive littoral plants from America than from the Old World. Though no tropical drift has yet been found stranded on the coasts of these islands, yet it is not unlikely that future investigators may find some seed-drift from Central America on the most southerly coasts of the group, as on the south-east shores of the large island of Hawaii. It would only be stranded in the winter months and then probably in small quantities.

Summary of the Chapter.

(*a*) Since the effective operations of the currents are limited to the shore-plants with buoyant seeds or fruits, such plants forming but a small proportion of any flora, it must be acknowledged that, numerically speaking, the results of the dispersing-agency of the currents on plant-distribution in general are but slight.

(*b*) Yet the importance of the subject is by no means to be measured by a numerical scale of results, a line of inquiry being here opened up leading to fields of investigation full of promise for the student of plant-distribution.

(*c*) Whilst dealing with the relation between the distribution of shore-plants and the arrangement of the currents, it is quite legitimate to discuss the currents of the Pacific from the point of view of the botanist, who, after all, must take his cue from the drifting seed and the resulting distribution of the plant.

(*d*) The shore-plants of the Pacific islands that are dispersed by the currents being mainly Indo-Malayan in origin, it follows that they have extended eastward over the Pacific to the Tahitian islands against the stream of the South Equatorial Current and against the trade-wind. It is, however, shown that they could have availed themselves of the interval between January and March when the North-west Monsoon reaches the Pacific.

(*e*) It is claimed that whilst the mangroves and their associated plants have for the most part entered the Pacific by the Melanesian route through the Solomon Islands, the beach-plants have also followed the route through Micronesia by the Caroline, Marshall, and Ellice Groups.

(*f*) A small number of the strand-plants of the Pacific islands that are dispersed by currents occur in America as well as in the Old World; and questions of prime importance arise when we have to decide whether their home is in the Old World or in the New World.

(*g*) Good reasons are given for regarding them as chiefly of American origin; and it is shown that America with regard to the arrangement of the currents stands in the singular relation of being a disperser but not a recipient of shore-plants.

(*h*) It is pointed out that the tropical shore-plants that are distributed by currents belong to two great regions which are the effect of the present arrangement of the currents, viz., the American including the West Coast of Africa, and the Asiatic comprising the remainder of the tropical zone. Each region has its own plants, and those that occur in both, being in fact distributed all round the tropics, are regarded, according to the principle above stated, as having their home in the American region.

(*i*) The occurrence of the same strand species on the Pacific and Atlantic coasts of tropical America is regarded as indicating that the arrangement of the existing species of its shore-plants, more particularly of the mangroves, antedates the emergence of the Panama Isthmus. This hypothesis is not needed for the coast plants like Entada scandens that occur inland, since we can now observe their seeds being carried down into the Atlantic and Pacific Oceans by rivers draining the opposite slopes of the same "divide" in the Panama Isthmus.

(*j*) It is shown that the currents of the Pacific have failed to establish the numerous beach-trees (possessing buoyant fruits) of the Pacific islands, not only in the Hawaiian Group, but also on the coast of America; and it is therefore argued that we should expect the Hawaiian Group to have received through the currents its shore-plants with buoyant seeds or fruits from the tropical west coasts of America.

(*k*) In support of this contention it is pointed out that most of the Hawaiian strand-plants that are dispersed by the currents are found in America, and some indeed in America to the exclusion of the Old World.

(*l*) The arrangement of the currents in the North Pacific also favours the view that the Hawaiian Islands are more likely to receive plants by the agency of the currents from America than from the Asiatic side of the Pacific.

CHAPTER IX

THE GERMINATION OF FLOATING SEEDS

Germination in the floating seed-drift of tropical estuaries.—A strain of vivipary.—Abortive germination of seeds in warm seas.—A barrier to plant dispersal.—The borderland of vivipary.—Summary.

THE tendency of the floating seed or fruit to germinate in the estuaries of tropical rivers is especially characteristic of the plants of the mangrove-swamps and of their borders. In the Fijian rivers, and particularly in the estuary of the Rewa, where the river-water is usually mixed with that of the sea, there are frequently to be found in a state of germination floating fruits of Barringtonia racemosa, Carapa obovata, Clerodendron inerme, Derris uliginosa, Smythea pacifica, &c.; whilst the floating fruits of more characteristic beach-trees like Barringtonia speciosa and Cerbera Odollam, that grow also on the sides of the estuaries, were never noticed in this condition. That this tendency should be restricted to the plants of the mangrove-formation and is not to be observed in the beach-trees is a singular fact. There is, however, an intermediate group of littoral plants mostly belonging to genera of the Leguminosæ and Convolvulaceæ, such as Mucuna and Ipomea, where germination of the floating seed is apt to begin but ends abortively, and results in the sinking and death of the seed. The subject of the germination of seeds in the floating drift of tropical estuaries presents itself, therefore, in three aspects:—

(1) As concerning the plants of the mangrove-formation, where, excluding the viviparous species (when germination takes place on the plant), germination is frequent in the water:

(2) As concerning the beach-trees where it is rare or absent altogether:

(3) As concerning certain Leguminous and Convolvulaceous

littoral plants where germination is not infrequent but always abortive.

Dealing first with the plants of the mangrove-formation, it may be remarked that the same tendency of the floating fruits or seeds to germinate, which is above noticed in the case of the estuaries of Fiji, came under my observation in the floating drift of the estuary of the Guayaquil River in Ecuador, the germinating fruits and seeds being carried far out to sea. The seeds of Anona paludosa, which float in quantities in the river-drift, were often found germinating; and the same may be said of the fruits of Laguncularia racemosa and of the "joints" of Salicornia peruviana which abound in the creeks of the mangrove-delta and are carried out to sea in the germinating condition.

It might be expected that this readiness to germinate in the brackish water of estuaries would prove to be a formidable obstacle to the dispersal of these plants over wide tracts of ocean. The exposed portions of the seedling might be deemed ill-suited to withstand, without injury, the "wear-and-tear" of transport by currents over long distances, even when not affected by the sea-water; and it might be thought that they would be often nibbled off by fish or destroyed by other aquatic animals. Only the specially organised seedlings produced by a viviparous process on the tree, such as those of Rhizophora and Bruguiera, might be regarded as able to survive the effects of prolonged immersion in the oceanic currents.

Observation, indeed, shows that such seedlings are exposed to and suffer from these perils; yet it is evident from the distribution of the species that, whether in the germinating condition or not, the seeds and fruits of Anona paludosa and Laguncularia racemosa have been carried by the currents from America to the West Coast of Africa. The seedlings of Avicennia and of Rhizophora mangle have also performed the same trans-Atlantic voyage. Those of both these mangroves are to be observed floating off the coasts and in the estuaries of both coasts of America. The seedlings of Avicennia are particularly abundant in the mangrove-creeks of the delta of the Guayaquil River; and I observed them in a healthy condition, ten to twenty miles out at sea, floating together with those of the Rhizophora. Since, as in the case of Rhizophora, germination occurs normally on the plant, Avicennia can only be dispersed by its floating seedlings. Yet it is noteworthy that although Avicennia seedlings appear, to a marked degree, less fitted for ocean transport than those of Rhizophora and Bruguiera,

the species have a much wider distribution. Avicennia officinalis has a cosmopolitan distribution in the tropics and beyond, occurring as it does on the Atlantic and Pacific coasts of America, on both coasts of Africa, over Asia and Australia, as well as in New Caledonia and New Zealand, but not in Polynesia (*Bot. Chall. Exped.*, III., 178). . . . . . I have now gone far enough to show that the tendency displayed by the seeds and fruits of several of the plants of the mangrove-formation to germinate either on the tree or in the floating drift of estuaries has not affected the general distribution of the species in its main outlines. Few fruits are found more often in a germinating condition in the floating drift of the Rewa River in Fiji than those of Barringtonia racemosa, yet the species ranges from the African East Coast eastward to Polynesia. Seedlings as well as seeds or fruits, whether or not in a germinating condition, are, therefore, able in such cases to disperse the species.

This readiness of the floating fruits of plants of the mangrove formation (excluding the viviparous species) to germinate in the estuaries is, I am inclined to think, due in the main to the strain of vivipary that runs through nearly all the plants of the mangrove-swamp and of its borders. It would, indeed, appear that the viviparous habit (the capacity of germinating on the plant) which finds its extreme development in Rhizophora and Bruguiera of the Fijian swamps is represented in its earliest stage in the readiness of the floating fruits of Barringtonia racemosa, Carapa obovata, &c., to germinate in the Fijian estuaries, and as remarked in Note 37 there is a suspicion of vivipary in the instances of both the species just named. Intermediate cases, as that of Laguncularia in the Ecuador swamps, occur in other regions with species where germination only takes place at times on the plant. This subject is, however, generally discussed in Chapter XXX. and need not be further dealt with here.

A predisposing cause of the germination of floating seeds and fruits in tropical estuaries would seem to be afforded by the super-heating of the water of the estuary. This came under my notice both in the Rewa River in Fiji and in the Guayaquil River in Ecuador, where the water of the estuary is often noticed to be some degrees warmer than that of the sea outside, and of the water from the river above the estuary. (See Note 38.)

We come now to the subject of the non-germination in tropical estuaries of the floating fruits of the beach-trees, such as Barringtonia speciosa and Cerbera Odollam, that in the Pacific islands

may contribute to river-drift. Such trees may grow on the banks of the estuary, and their fruits would thus readily fall into the water; but in the Rewa estuary in Fiji it was evident that the fruits and seeds of beach-plants, such as Scævola Koenigii, are also brought in by the tide. The seeds of Morinda citrifolia were often noticed in the Rewa drift together with the fruits of Heritiera littoralis, which is both a beach and a swamp plant, but never in a germinating condition. The same remark applies also to the fruits of beach trees found afloat in the sea between the islands, such as Cordia subcordata, Guettarda speciosa, and Terminalia. It is possible that a few of these plants, as in the case of Barringtonia speciosa, display traces in the structure of their fruits of a lost viviparous habit. (See Note 50.) It is pointed out in discussing Guettarda that germination is much more easily induced than one would expect in the case of fruits with such a hard ligneous putamen.

An interesting subject is presented in the abortive germination of the floating seeds of many plants of the Leguminosæ and Convolvulaceæ both at sea and in a tropical estuary. My conclusions on this matter are based partly on observations made in Fiji, but mainly on the results of numbers of experiments, this being unavoidable, since the abortive germination causes the sinking of the seed. The principal determining cause of the germination in water of one of these floating seeds is evidently to be sought in the temperature of the water, it being immaterial for the earliest stage of germination, as many of my experiments indicate, whether the seed or fruit is afloat in the sea or in the river. In these flotation experiments, when conducted under warm conditions with sea-water, the earliest signs of germination were frequently displayed in the softening, swelling, and sinking of the seed. If the swelling seed is taken out in time and planted after a preliminary soaking in fresh water, the germinating process is at once resumed and is often successfully and rapidly completed; but if the seed is allowed to remain in the vessel after it has absorbed sea-water the vitality of the embryo is destroyed and the seed decays.

That many seeds would fail from this cause to cross an ocean my experiments repeatedly demonstrated. Nor does the appearance of a seed afford any indication of its probable failure to cross an ocean. Some seeds of Mucuna, as far as their hard coverings could guide one, would seem to be quite secure from such a risk. The stony seeds, for instance, of M. urens D.C. look

as if they might safely be transported by the currents round and round the globe; and De Candolle very rightly placed this species in his scanty list of plants dispersed by currents. Yet few seeds are more treacherous when their buoyancy in sea-water is tested in a warm place, as in a hot-house. They may take up water, swell, and sink in a week, or they may float unharmed for a year.

The seeds most exposed to this risk are those of the Leguminous giant climbers, the lianes of the coast and inland forests of the islands of the tropical Pacific. They belong to the genera Mucuna, Strongylodon, &c.; and thus several of the plants that constitute for the student of plant-dispersal the enigmas of the Pacific are here included. The seeds of Mucuna are especially liable when afloat in sea-water under warm conditions to display the early signs of germination, swelling up and sinking to the bottom of the vessel, a process, however, soon arrested and followed by the death of the embryo unless the seed is removed in time. Yet the seeds of this genus are notably long "floaters." Those of an American species, variously designated as Mucuna pruriens D.C. and M. urens D.C., have long been known to be washed ashore together with the seeds of Entada scandens on the western shores of Europe, and particularly on the Scandinavian coast, where they form regular constituents of what the Scandinavian botanists correctly term the Gulf-stream Drift.

Mucuna urens D.C. occurs with other American shore-plants that are dispersed by the currents on the African West Coast; and there is no reason to doubt that its seeds perform the trans-Atlantic voyage. It is found in Polynesia, in Hawaii, in the Marquesas, and according to Reinecke also in Samoa; and probably it occurs in other groups. The specific determinations of the genus, however, need thorough overhauling, so that it is not possible to deal more than in general terms with the distribution of a species. The distribution of Mucuna urens in the Pacific is, however, irregular, and no doubt this is to be connected with the uncertain behaviour of its seeds when transported by tropical currents. The seeds would, I venture to think, often sink through abortive germination in the warm areas of equatorial seas.

When in Hawaii I kept ten of the seeds of this species (M. urens D.C.) in sea-water for four and a half months, none of them sinking in that period, the temperature of the water rarely reaching over 80°F., the average daily temperature being 76—77°. However, when four years afterwards in England I placed five of the seeds obtained at the same time in sea-water under conditions

where the water-temperature ranged for the first few weeks between 75° and 90°, three of them began to swell within ten days, and on removal at once germinated healthily. The remaining two were afloat at the end of twelve months, and when planted one of them germinated a month afterwards.

Having experimented on the seeds of about half a dozen different species of Mucuna in sea-water, all with buoyant qualities, it is possible for me to lay down the general rule for the buoyant seeds of the genus that sinking is the result of an attempt at germination, which, as before observed, proves abortive unless the seed is removed in time. It is obvious that the gardener wishing to raise plants of this genus without delay might profitably adopt the method of keeping them afloat in water at a temperature of 80—90° F. until they begin to swell, which may happen in some cases in a few days. Sea-water seems to produce the most rapid results.

When on Keeling Atoll in the Indian Ocean I collected, amongst the stranded seed-drift brought by the currents to those islands, the seeds of five or six species of Mucuna, two of which were identified at Kew as M. macrocarpa, Wall., and M. gigantea D.C. (see my paper on the dispersal of plants at Keeling Atoll). No plant of this genus appears up to that time to have been recorded from the Keeling Islands, so that at all events most if not all of the seeds had been brought by the currents from the Indian Archipelago, some 700 miles away. It may be added that amongst the drift gathered by me on the south coast of Java the seeds of three species of Mucuna were identified at Kew, including the two above-named species from Keeling Atoll.

These current-borne seeds of the Keeling beaches had probably performed an ocean journey of a thousand miles, since the route could scarcely have been direct. Yet their behaviour when placed eighteen months after in sea-water in a hothouse in England was most erratic. Of three seeds of Mucuna gigantea all swelled and sank within eight days. Two seeds of M. macrocarpa sank after floating from sixty to a hundred days; whilst of two seeds of another species both remained afloat after a year. In a sea-water experiment in England on five Hawaiian seeds of M. gigantea, under the conditions referred to in the Mucuna urens experiment, one sank within ten days, whilst three of them were afloat after twelve months, one of them subsequently germinating. This species, it may be remarked, is widely distributed as a coast plant over tropical Asia, Australia, and in Polynesia. It seems to take

the place in the Old World which Mucuna urens takes in America, and it is curious that they meet in Polynesia, being sometimes associated as in Hawaii. In the chapter on my observations in Ecuador and in Panama it is remarked that Mucuna seeds are frequent constituents of river, sea, and stranded drift. I, therefore, have enjoyed the opportunity of observing the behaviour of the seeds of this genus in a variety of localities, namely, in the Keeling Islands, in West Java, in Fiji, Hawaii, and tropical America ; and this may be pleaded as an excuse for entering into so much detail respecting them.

The large seeds of Strongylodon lucidum (S. ruber), a Leguminous liane that ranks with the species of Mucuna amongst the huge climbers of the forest of the Pacific islands, behaved in a similar way in my flotation experiments in sea-water. Though, as shown in Note 3, these seeds can float for a year and retain their germinating power, some of them brought their buoyant capacity prematurely to an end by an abortive attempt at germination. These black rounded seeds form a common object amongst the river seed-drift stranded on some of the Fijian beaches in the vicinity of estuaries. They are so hard and durable that they are mounted in brooches in Honolulu. Yet these pebble-like seeds will sometimes begin to swell in a few days in sea-water. Out of five seeds placed in sea-water in England under warm conditions (the water temperature for the first few weeks ranging between 75° and 90° F.), one swelled and sank within ten days, another did so after two months, whilst the other three were afloat after twelve months, and one of them subsequently germinated. There is some disagreement amongst botanists as to the limits of the specific characters of the plants of this genus (see Note 39); but the plan seemingly most in accord with the fundamental principles regulating plant-distribution in this region of the Pacific is to regard the forms found in Hawaii, Tahiti, and Fiji, as referable to one species. In addition to the Polynesian forms there are only two or three species, found in the Philippines, Madagascar, and Ceylon, and it is with the species from the last-named locality that the Polynesian species is by some identified.

The seeds of several other Leguminous climbers would probably act in a similar way, for instance, those of Entada scandens ; but the seeds of this plant experimented on by me were too few to enable an opinion to be formed. Of four seeds of Dioclea violacea from Fiji that were subjected to the same experiment as those of Strongylodon lucidum, all floated in sea-water after a year, with

the exception of one that did not swell and sink until after ten months. On the other hand, in my experiment in Fiji on the fresh seeds of Canavalia obtusifolia, a plant found on tropical beaches all round the globe, seventy per cent. sank in the first six or seven weeks, swelling and displaying the first signs of germination, but quite ten per cent. were afloat after three months.

My experiments on the foregoing and other littoral species of the Leguminosæ merely indicate that under the ordinary temperature of tropical currents a portion of the seeds will probably sink owing to abortive attempts at germination. It is likely that if in the experiments in England a constant temperature of 85° to 90° F. had been sustained throughout, most if not all of the seeds would have swelled and sunk within a month or two. The temperature of the experiments in Fiji and Hawaii did not exceed that of many tropical currents; but there are areas of superheating in equatorial seas, which I think would prove insurmountable barriers in the path of most drifting Leguminous seeds, a subject to which further reference will be made.

Coming to the Convolvulaceæ, my experiments show that the buoyant seeds often lose their floating powers from the same cause. Those of Ipomea pes capræ may be taken as an example. I was surprised to find when experimenting on the buoyancy in sea-water of these seeds in Fiji and Hawaii that a considerable proportion, about a third, sank in the first two months, swelling and sinking to the bottom. That this swelling represented the early stage of germination was well brought out in parallel experiments in fresh water and sea-water made in England on the buoyant seeds of the British littoral species, Convolvulus soldanella. A good proportion of the seeds in the first part of the experiment absorbed water, swelled, and sank, those in fresh water proceeding at once to germinate healthily at the bottom, whilst those that sank in sea-water merely decayed. Of the survivors about fifty per cent. in either case floated after six months. It may be added that the seeds of other tropical littoral species, such as those of Ipomea glaberrima and I. grandiflora, behaved in the same way.

It would appear from my experiments, and it is a result that we should expect, that buoyant seeds of the Leguminosæ and Convolvulaceæ would often float for much longer periods under cool than under warm conditions. There must be areas of high temperature in mid-ocean that would prove much more fatal to the chances of a drifting tropical seed than the icy waters of a Polar current. In my paper on Keeling Atoll I have described how I

procured the germination of a seed of Ipomea grandiflora, Lam., after a year's flotation in sea-water in London, which included a period of three weeks when the water temperature was at or about 32° F. These seeds from this point of view would be exposed to much more risk of sinking through abortive attempts at germination when drifting across some parts of the Pacific Ocean. It would appear from the Admiralty Chart of Surface-Temperatures, published in 1884, that such an area with a surface-temperature of 83° to 86° throughout the year extends north and east of New Guinea well into the Pacific, reaching in the first half of the year as far east as the Tahitian region. It would seem highly probable that the immersion of Leguminous or Convolvulaceous seeds for many months in these tepid waters would in most if not in all cases induce incipient germination which would lead to the sinking of the seed. There are, however, exceptional cases, as that of Cæsalpinia bonducella, which, as my experiments recorded in Chapter XVII. indicate, appear to be quite proof against any conditions of temperature such as are likely to be found in tropical seas in the present day.

There are a few general considerations arising out of the foregoing observations to which reference may now be made. The study of the behaviour of the floating seed or fruit often carries us, as I have before implied, to the borderland of vivipary. When from a canoe on a Fijian river we lift up the germinating fruit of Barringtonia racemosa from amongst the drift floating past in the stream and pull down from the branches overhead the seedling a foot in length of Rhizophora, we hold in our hands the two extremes of the series of vivipary. With many of the plants of the mangrove-formation there is a fine adjustment with respect to the germinating capacity of the seed, or in other words a delicate balancing of organisation on one side and of physical conditions on the other. A slight disturbance of the equilibrium would produce great results in plant distribution. Thus, an elevation of the temperature of the sea-water in the tropics to 90° F. would, I apprehend, produce the abortive germination of nearly every floating seed and fruit in equatorial seas, even of those of the beach-trees like Barringtonia speciosa and Terminalia littoralis that are regarded as proof against such risks under existing conditions where the surface-temperatures would average 78° to 80°.

There would thus be a barrier to the dispersal of plants by currents as effective as that of a frozen ocean. In the warm, humid climates of the early geological ages, seed-transport by currents

may have been often impossible, since the seeds that did not begin to germinate on the plants of the swamps would probably do so in the tepid water of the sea. Viviparous plants would, however, be placed at no greater disadvantage than they are at present, since the genera Rhizophora, Avicennia, and others are now only dispersed by the floating seedlings. But such an increase of temperature at the present time would mean the death in the current of the floating seeds and fruits of nearly all non-viviparous shore-plants. As a rule every Leguminous and Convolvulaceous seed would swell up and go to the bottom; whilst fruits like those of Barringtonia racemosa and Carapa obovata, that often germinate afloat in tropical estuaries, would invariably do so under the changed conditions, and the seedlings not being adapted for ocean transport would perish.

Yet we know that with the seeds of many inland plants temperature has seemingly very little to do with starting the process of germination. We are familiar with the fact that the seeds of many plants that fail to germinate in the summer of their production habitually germinate under apparently less favourable conditions of temperature in the following spring. This is attributed by botanists to the immaturity of the seed on first falling from the plant, a further period of maturation being necessary before, under any conditions, germination is possible.

We see this also well illustrated in the floating seeds and fruits of the Thames drift. Most of them fail to germinate in the drift at the end of the summer and the beginning of autumn, and defer the process until the following spring, when they germinate freely in the water under much cooler conditions than those which they experienced in the early part of their flotation in the drift. There are, however, exceptions to this rule. Plants like Caltha palustris, for instance, are rarely represented in the spring seed-drift of ponds and rivers, because most of the fruits or seeds germinated soon after falling into the water in the previous summer.

In most of my sea-water experiments in England the immersion had a very marked influence, not in causing premature germination and destroying the germinating capacity, as often happens with the floating seeds of Convolvulaceæ and Leguminosæ, especially in the tropics, but in postponing without injury to the seed the process of reproducing the plant. Such seeds or fruits when placed in fresh water after many months of flotation in sea-water germinated very freely in a few days, whilst those left in the sea-water under precisely the same conditions remained unchanged. This is true of many of

the seeds and fruits found in the Thames drift, such as those of Ranunculus repens, Lycopus europæus, Rumex, &c. A striking instance was also afforded by the seeds of Arenaria (Honckeneya) peploides, where seeds transferred directly to fresh water, after many months flotation in sea-water, germinated in a few days; whilst those left in the sea-water remained unchanged. This subject is discussed at length in Note 19, and needs no further mention here.

If the seeds of many plants in Great Britain postpone through immaturity their germination to the following or even to the second spring, it goes without saying that this does not exclude temperature as the ultimate determining factor in germination. The immaturity of seeds adds another link to the series of the germination-range in plants. This range begins with the plants where germination takes place on the tree and the seedlings hang suspended from the branches, as in the typical mangroves Rhizophora and Bruguiera. Here, as is shown in Chapter XXX., there is evidently no period of repose between the completion of the maturation of the seed and the commencement of germination. The range ends with the detachment of immature seeds which ripen apart from the parent plant, and may postpone the germinating process for months and often for years. All intermediate stages exist between these two extremes. Thus the seedling may at once detach itself from the parent as in Avicennia, or the germinating process on the plant may be limited to the protrusion of the radicle as in Laguncularia, or the seeds may be quite mature and ready to germinate as soon as they fall to the ground, as we find with many small seeded plants. All the stages, of which only a few are here indicated, are full of suggestiveness for the student of plant-life.

This subject is dealt with from other standpoints in Chapter XXX., but the reader will now see more clearly what was meant when I said that the study of the behaviour of the floating seed leads us to the borderland of vivipary. In this range of the germinating process we may possess an epitome of the history of the climatic conditions of plant-life from an early era in the world's story, beginning with those ages when perhaps under the uniform conditions that then prevailed, all plants were more or less coast-plants and more or less viviparous, and coming down to the present era when with an extensive and varied land-surface there is great variety both in climate and in the range of germination. The mangrove-swamp and its viviparous trees would thus represent from this point of view a condition of things once more or less universal on the globe.

Summary of the Chapter.

(*a*) The tendency of the floating seed or fruit to germinate in the brackish water of tropical estuaries is especially characteristic of the plants of the mangrove-swamp and their vicinity; but with those of the beach trees that occur in the river-drift it is rarely if at all to be observed.

(*b*) From the wide distribution of plants of the mangrove-formation it is evident that this readiness of the floating seed or fruit to germinate is not prejudicial to the dispersal of the species.

(*c*) It may perhaps be in the main attributed to a strain of vivipary running through all the plants of the mangrove-formation, which finds its extreme development in the viviparous species, where germination takes place on the tree. But it is probably favoured by the superheating of the waters of tropical estuaries.

(*d*) In the case of the buoyant seeds of several climbers and creepers of the Leguminosæ and Convolvulaceæ, more or less littoral in their station, it is shown that in warm water, whether fresh or salt, a good proportion are apt to sink through incipient germination, which results when the experiment is made in sea-water in the death of the embryo.

(*e*) Though in tropical currents of ordinary temperature a good number of such floating seeds would escape this risk, it is argued that there are certain warm areas in the tropical seas that would prove much more fatal to the chances of these drifting Leguminous and Convolvulaceous seeds than the icy waters of a polar current. It is thus held that these seeds often sink in mid-ocean in tropical latitudes through abortive germination.

(*f*) The study of the behaviour of the floating seed or fruit leads us to the borderland of vivipary. In the scale of the germinative capacity of plants it is possible to arrange a continuous series that commencing with the mangroves, where germination takes place on the tree, ends with those numerous inland plants where seeds are liberated in an immature condition.

(*g*) It is suggested that the viviparous habit may have been the rule under the uniform climatic conditions of early geological periods and that with the differentiation of climates that marked the emergence and extension of the continental areas the viviparous habit has been lost, except in those regions of the mangrove-swamps which to some extent retain the climatic conditions once general over the globe. With differentiation of climate the true seed-stage with its varying rest-periods has been developed.

CHAPTER X

THE RELATION OF THE BUOYANCY OF SEEDS AND SEED-VESSELS TO THE DENSITY OF SEA-WATER

The general principles concerned.—The subject assumes a statistical character. —Seeds and seedvessels are as a rule either much heavier than sea-water or much lighter than fresh water.—The present littoral plants with buoyant seeds or seedvessels could be equally well dispersed by currents in oceans of fresh water.—Seed-buoyancy has no relation either in the present or in the past to the density of the sea.—Though an accidental attribute, the specific weight of seeds has had a profound influence on plant-distribution.—Summary.

To find amongst the results of my numerous experiments examples illustrating the influence of density on flotation has not been so easy as I at first imagined. Excluding all adventitious causes of buoyancy, a matter discussed in Note 40, it may be inferred that the great majority of seeds and fruits sink both in fresh water and sea-water. Of those that are buoyant many float indefinitely in both waters, whilst in a very few cases, where the floating power is derived from an outer fleshy covering, as with the fruits of Potamogeton natans, the fruits float a much shorter time in sea-water than in fresh water, on account of the injurious effect of the salt upon their coats.

Experiments have to be specially directed towards this subject. It would be useless to experiment in fresh water at one time and in sea-water a month later. Nor would it answer to employ seeds and fruits from different localities, since variations in this way sometimes occur. It is necessary that the experiments should be made on seeds or fruits collected at the same time and place, and that they should be simultaneous and carried on under the same conditions. As the discussion proceeds, the reader will perceive that many interesting points are opened up, and that such

an investigation, instead of being, as the title of this chapter might suggest, an abstruse and disconnected inquiry, is of considerable importance in relation to the dispersal of plants through the agency of currents.

Guided by the results of my experiments in this direction I will proceed to lay down certain general principles :—

(A) In the first place it may be accepted as a general rule that *seeds or seedvessels that sink in fresh water sink also in sea-water,* the difference in density between the two being rarely a factor of any importance in determining buoyancy. The great majority of seeds and fruits come under this category, since, as is pointed out in Chapter VIII., only a small proportion of the whole, say a tenth, possess floating power. We might cite, as illustrative of this principle in temperate regions, almost all the 240 species included in the non-buoyant group of the British plants experimented on (see Chapter III. and Note 10). As a general rule this is true alike of the small seeds of the Cruciferæ and Scrophulariaceæ, of the nutlets of the Labiatæ and Boragineæ, of the genus Scirpus, and of the dust-like seeds of Juncus. The results of my experiments on the plants of the tropical Pacific are no doubt typical of other tropical regions ; and if I wished to quote instances, I should have to enumerate not only most of the plants without buoyant seeds or fruits that are mentioned in the Fijian and Hawaiian lists given under Notes 2, 4, and 6, but also to appeal to tropical regions generally.

(B) One can carry the principle above-named yet further and say that not only as a rule do seeds or fruits that sink in fresh water sink also in sea-water, but that so far as tested *many of them sink in water of much greater density than that of ordinary sea-water* (1·026). Thus, for instance, the seeds of Nuphar luteum, Scrophularia aquatica, and Stellaria aquatica, the nutlets of Polygonum persicaria, and the achenes of Aster tripolium sank in sea-water the density of which had been raised to 1·050, the limit of the experiment. The minute seeds of Juncus communis and J. glaucus and the larger seeds of Luzula campestris, even after drying for six months, sank in salt water having a density of 1·075. It would, however, seem probable that for most of these small seeds and seedvessels a density of 1·100 would prove to be the critical point. If this is so, then most of those that sink in sea-water would float in the dense water (1·160) of the Dead Sea.

However, my investigations have only gone a small way in this direction ; and perhaps some of my readers will pursue the

inquiry. I will take the case of the nutlets of Scirpus palustris. They sink in fresh water and in sea-water, or may float in rare cases for a day or two. Out of 100 of these seed-like fruits, 25 floated in salt water of a density of 1·075, 13 in water of 1·050, 7 in sea-water (1·025), and 3 in fresh water, (1·000). It would thus appear that the proportion of buoyant nutlets is doubled with every increase of ·025 of the density scale. At this rate of increase they would all float in salt water of a density of 1·125, which may be regarded as the suitable medium for the flotation of the fruits of this Scirpus. . . . The seeds of Glaucium luteum, the Sea-Poppy, have no buoyancy either in fresh water or in sea-water even after prolonged drying. They all sank in water of a density of 1·050, but 18 per cent. floated when the density was raised to 1·075. At the rate of increase noticed in the case of Scirpus palustris, all the seeds would float in water of a density of 1·130–1·140. . . . The acorns of the Common Oak (Quercus robur) have usually but little buoyancy unless they have been long drying. After soaking in fresh water for half an hour 100 mature fruits, without the cupule, that had been kept a fortnight, I found that only 2 floated in fresh water, 6 in sea-water (1·025), and 18 in water of 1·050. At this rate of increase all would float in water having a density of 1·080–1·090.

(C) There is also another general rule, and it is this :—*Seeds or fruits that float for a long time in sea-water usually float almost as long in fresh water.* Here belong the greater number of buoyant seeds and fruits, those only able to float for a few weeks being comparatively few. Now with the long-floating seeds and fruits, those for instance that float in the drift of English rivers from the autumn to the spring, or those that are transported by currents over the tropical zone, there is, as a rule, but a slight difference between their flotation periods in fresh water and sea-water. If one of them sinks after floating for several months in fresh water, it will sink in sea-water a few days after. Fruits of Scævola Kœnigii, pyrenes of Morinda citrifolia, and seeds of Thespesia populnea, Ipomea grandiflora, Cæsalpinia bonducella, and of different species of Mucuna, that had been kept afloat for a year in sea-water, floated just as buoyantly in fresh water at the close ; and in those cases where any sank during the course of the experiment, it was ascertained that they were able to float in fresh water almost to the end.

That many of the seeds and fruits of tropical littoral plants

that are known to be dispersed by the ocean-currents will float well in fresh water is shown in the constant occurrence in the floating drift of Fijian estuaries, where the water may be quite fresh or brackish, of the seeds and fruits of plants like Cerbera odollam, Clerodendron inerme, Entada scandens, Heritiera littoralis, Ipomea pes capræ, Morinda citrifolia, Mucuna, Vigna lutea, &c. In the same way I noticed afloat in the Guayaquil River in Ecuador, when the water was quite fresh, seeds and fruits characteristic of the sea-drift, such as those of Anona paludosa (seeds), Entada scandens, Ipomea, Mucuna, Vigna, &c.; and when we supplement observation with experiment, as for instance in the case of Anona paludosa, we find that they will float equally long in fresh and sea-water.

The same rule prevails with most of the buoyant seeds and seedvessels of plants of the British flora—seeds and fruits, as I may remind the reader, that are mostly to be found in river and pond drift. I am not able to distinguish any difference of importance in the results of the separate fresh-water and sea-water experiments. Thus with the seeds or seedvessels of Bidens cernua, several species of Carex, Galium palustre, Iris pseudacorus, Lycopus europæus, Ranunculus repens, and numerous others, the difference after a flotation of many months was but slight. If the results of the separate experiments were to be compared, there would be at least ninety afloat in fresh water for every hundred afloat in sea-water; and if at the end of a sea-water experiment, whether occupying three, six, or twelve months, the seed or fruits were to be placed in fresh water, quite nine-tenths and sometimes more would remain afloat. A striking illustration of the principle that the excess in density of sea-water, as compared with fresh water, adds but little to the floating capacity of seeds is to be found in the results given in Note 41 of simultaneous experiments made some years since by Mr. Millett and myself at Marazion and in London on the seeds of Convolvulus soldanella.

(D) In their relation, therefore, to the density of fresh water and sea-water, most seeds and seedvessels may be placed in *two principal classes, the first including quite four-fifths of the total, where they are much heavier than sea-water, and the second comprising most of the remainder, where they are much lighter than fresh water.*

(E) It would be surprising, however, if there were not some seeds or seedvessels that come between these two extreme

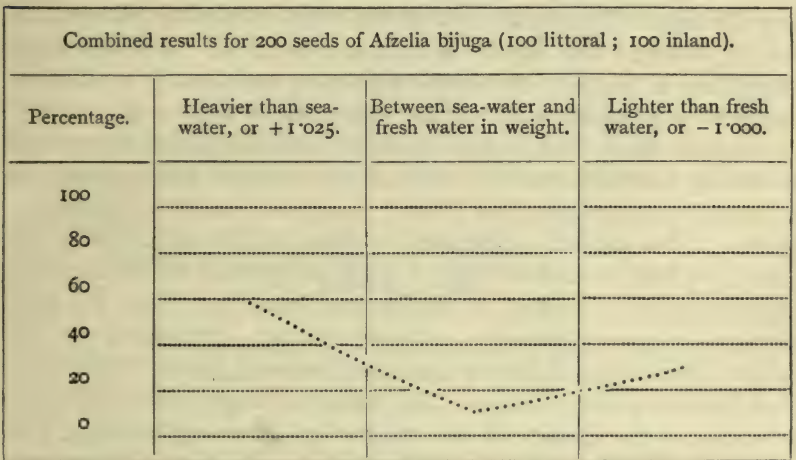
groups; some, indeed, that have a specific weight approximating to that of fresh water, or to that of sea-water, or fluctuating between them, and presenting such evidence of a fine adjustment that the observer, forgetting that they are members of a series, might be apt to regard them as specially adaptive in their origin. It will thus be seen that this subject is gradually assuming a statistical character; and in truth we shall ultimately recognise here the play of the laws of numbers.

As an example of the plants where the specific weight of the seeds or fruits is near that of fresh water, Alisma plantago may be taken. In the course of an experiment, by lowering the density of the water from 1·025 to 1·020, I sent a shower of floating carpels to the bottom. The results vary considerably, as one might expect; but, generally, during the first few days of an experiment about twice as many (sometimes in all as much as 80 per cent.) sank in fresh water as in sea-water, a few only floating in either water for long periods. . . . The seeds of Arenaria peploides present an example where the specific weight is between that of fresh water and of sea-water. For the purposes of dispersal they may be considered as heavier than fresh water and lighter than sea-water. The details are given in Note 18; but it may be remarked here that plants possessing seeds or fruits that sink in fresh water and float in sea-water are very rare. As indicated below, this is what we might look for on statistical grounds.

Plants whose seeds or fruits are not much lighter than sea-water are exceptional. In such cases the effect of increased density of the water is to extend the period of flotation. Thus, in my experiments on the nutlets of Scirpus maritimus, the majority of the fruits floated in fresh water only eight to ten days; whilst in ordinary sea-water they floated in most cases two to three weeks; but when the density was raised to 1·050, the greater number of them were afloat after two months. In a few plants, as with Spiræa ulmaria, the effect of the difference in density between fresh and sea-water was not to extend the period of flotation, but to increase the number that floated for a given period, the extreme limit of the buoyancy of the carpels in either water with this species being about three weeks.

Amongst tropical plants, as illustrated by those of the Pacific islands, cases also came under my notice where the mean specific weight of the seed is somewhere between those of fresh water and sea-water. The seeds of Afzelia bijuga, an inland as well as a

littoral tree in Fiji, offer an interesting example. If we place 100 seeds of a littoral tree in sea-water, we find that on the average about 70 float. If then we lower the density gradually, some of the seeds begin to sink at once; and on the removal of the survivors to fresh water, about 47 will remain afloat. The results may thus be stated:—Out of 100 littoral seeds, 30 are specifically heavier than sea-water (1·025); 23 are between sea-water and fresh water in specific weight; whilst 47 are lighter than fresh water (1·000). When, however, we take 100 seeds of inland trees, we find that on the average 87 are heavier than sea-water, 5 are in weight between sea-water and fresh water, and 8 are lighter than fresh water. The significance of these figures becomes evident when we arrange them in curves. The combined result for littoral and inland seeds is given in the diagram below;



and we see there, what is also indicated with the separate curves that we are dealing with a double series, one concerned with seeds lighter than fresh water, and the other with seeds heavier than sea-water. The reader can himself supply the separate curves for the littoral and inland seeds. The point, however, to notice is that if a botanist with a statistical bent were to make a miscellaneous collection of the seeds of the Vesi (Afzelia bijuga) in one of the Fijian islands, in order to test their buoyancy, he would obtain such a result as is given in this diagram. Two varieties of the tree would be at once indicated, and further research would indicate that these varieties were connected with littoral and inland stations. This subject is further dealt with in Chapter XVII.

It might seem strange that the seeds of Entada scandens should come into the category of seeds with a specific weight near that of fresh water ; yet my observations in Fiji indicate that such is the case. In the discussion of this plant in Chapter XVII. it is pointed out that, as a rule, not more than a fourth will float in a river when they are first freed from the pod, and not more than fifty per cent. will float in the sea. Those that float, however, in either water will usually float indefinitely. The seeds also of Mucuna gigantea D.C. are not very much lighter than fresh water. Out of six seeds that floated in sea-water buoyantly, five floated in fresh water, but heavily.

It is of interest to notice in this connection that the mangrove-seedlings produced by germination on the tree, as in the case of Rhizophora and Bruguiera, have a mean specific weight somewhere between fresh water and sea-water. This is often illustrated in a curious way, when the seedling has not been prematurely detached from the tree. Thus in the sea off the coast of tropical America, as well as amongst the Fijian Islands, the seedlings of Rhizophora mangle are as a rule to be observed floating horizontally ; whilst in the fresh or brackish water of the estuaries of these regions they assume a more or less vertical position, only the plumular portion protruding above the water. This is also true of the seedlings of Rhizophora mucronata, the Asiatic mangrove, and of Bruguiera rheedii. This subject is discussed in detail in Chapter XXX. ; but it may be here remarked that a good proportion of Rhizophora seedlings, when detached in the mature condition from the tree, have no buoyancy, between 20 and 50 per cent. going to the bottom when they fall into a river, and between 5 and 10 per cent. when they drop into the sea. The navigator might often obtain an indication of the density of the sea-surface when approaching the mouth of a large river by observing the floating Rhizophora seedlings (a foot long) which are carried out to sea in numbers. If he sees them from the deck of his ship floating horizontally he will infer that the surface-water is mainly sea-water. In ordinary fresh water when they float vertically he would not be able to distinguish them from floating seeds or fruits.

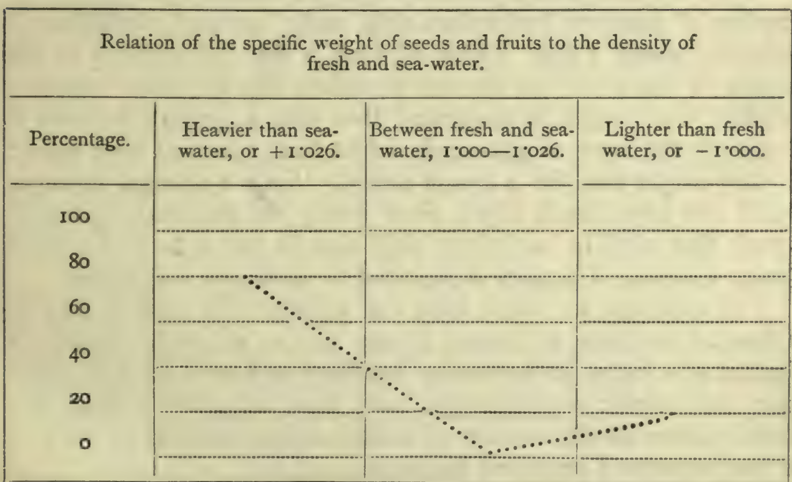
It has only been possible to treat this subject in an illustrative manner. More details might have been given ; but I have gone far enough to bring the following points into relief and to justify one in drawing the conclusions to be now stated.

Most seeds and seedvessels in respect of their floating powers tend to gather around two centres or means and to form two groups, the sinking group and the buoyant group.

In the sinking or non-buoyant group, which includes 80 *per cent. of the whole, the mean specific weight is considerably greater than that of sea-water* (1·026), *which would require its density to be raised to* 1·100 *in order to serve as a floating medium for many of them.*

In the buoyant group the mean specific weight is much lighter than that of fresh water (1·000)*; and from this it is to be inferred that in oceans of fresh water the same fruits and seeds in the mass would be distributed by the currents that are transported by them at the present day. Even though it arose from an ocean of fresh water, the coral island would receive the same littoral plants through the agency of the currents that it receives under its existing conditions.*

The number of plants with seeds or fruits between fresh water and sea-water in specific weight is very small, probably not over 2 per cent. of the total. Most seeds or fruits that sink in fresh water sink also in sea-water, and most that float in sea-water float also in fresh water. *Nature has thus created a wide gap between the sinking and the floating seed; and nearly all of the work of the present currents in plant-dispersal might have been effected, so far as the density is concerned, in fresh water.* She has not arranged seeds and seedvessels in what the statistician would term "a good series." As indicated in the diagram below, there are two series that meet in



the neutral region where the density is between fresh water and sea-water, but with culminating points placed on the one side far above the density of sea-water and on the other far below that of fresh water.

I do not, therefore, think that the buoyancy of seeds and fruits has had any relation either in the present or in the past to the density of the sea. Nor is it to be supposed that any slight variations in density in the course of ages would have materially affected the dispersal of plants by currents. It is to be inferred that the physicist and the geologist would be prepared to grant only small variations, such as a change from 1·020 to 1·025. It will be gathered from what has been said before that changes of this nature would have a very slight influence on the buoyancy of seeds and fruits, since the plants they would affect would be very few. The change that the student of plant-dispersal would require to produce any marked alteration in distribution would be in amount alarming to the physicist.

Whether or not the oceans have been getting fresher or salter in the course of ages (see Note 42), we will be moderate in our demands, and will listen to the physicist when he argues that a diminishing density, for instance, from 1·035 to 1·025, in the course of ages might explain some of the peculiar features in the present isolation of insular floras. Many seeds, he would contend, that could float across an ocean having a density of 1·035 would be unable to accomplish it when the density fell to 1·025. It has, however, been remarked that the critical point of density for the flotation of seeds or fruits that sink under present conditions is probably about 1·100. Cases of such a fine adjustment to the density of sea-water are too few to endow this argument with any weight. Or it might be suggested that with a gradual increase in density in the lapse of ages seeds might float now that sank before, or they might float for a longer period. Such a change, however, would not have much effect, since nearly all the seeds and seed-vessels that sink in our rivers sink also in our seas, and a much greater increase of density is required to make any difference.

Yet, although we might term the sinking of a seed or fruit an accidental attribute of certain plants, just as we might regard the floating of a log as an accidental attribute of a pine, since in either case the specific weight might have been acquired without any direct relation to the density of water, still the sinking of the seed or fruit signifies a profound distinction not only, as is stated below, in plant distribution, but, as we shall see later on, in plant-development. Especially striking, says Prof. Schimper (p. 153), is the dependence between an over-sea area of distribution and a station at the coast in the case of species of the same genus of which some belong to the littoral and some to the inland flora. In the first

place, as has been often remarked in these pages, we have a wide distribution generally associated with considerable buoyancy of the seeds or fruits. In the second case the areas are usually very restricted and there is little or no buoyancy. The better fitted a seed or fruit is for dispersal by currents the greater, therefore, is the area of the plant. Whether such an important relationship depends on an accidental attribute of the seed or fruit is the question that immediately presents itself. But it is obvious that in raising such a question we touch on a very vital point in adaptation, since if attributes developed in one connection have a profound influence in another we may have to rearrange some of our fundamental notions of the inner workings of Nature.

Let us, therefore, look a little closer into this matter, and turn again to the Pacific islands. The present state of things may be thus tersely described. Whilst the shore-plants dispersed by the currents have remained relatively the same, changes of all kinds, from the production of a variety and of a species to the development of a genus, have taken place in the inland floras. Now, let us imagine that all this is altered and that every seed or fruit is buoyant. There would then be but little distinction between the strand and inland floras, since they would be in a constant state of interchange, and most species would be widely distributed. A relatively monotonous aspect would belong to all insular floras, and indeed to much of the plant-world, since isolation, one of the principal conditions for the origin of new species and new genera, would often not exist.

On the other hand, let us suppose that all seeds and fruits were non-buoyant. The agency of birds would then be alone available for stocking new islands with most of their plants. The conditions of isolation would be intensified. There would be no widely-ranging strand-flora, since every island and every stretch of continental sea-board would possess its own littoral plants that could only reflect the peculiarities of the inland flora. The only determining factor between coast and inland plants would be the presence or absence of the capacity or organisation for occupying a station on the sea-shore.

We have now proceeded far enough to disclose the far-reaching influence on plant-distribution and on plant-development that the relation between the specific weight of seeds and fruits and the density of sea-water must possess. Yet it has been shown that when such a relation is viewed statistically it has an accidental aspect. We will accordingly devote the next few chapters to the

discussion of the buoyancy of seeds and fruits from the structural standpoint.

Summary of the Chapter.

(*a*) The great majority of seeds and seedvessels (quite 80 per cent.) are much heavier than sea-water, but a noticeable proportion are considerably lighter than fresh water, whilst those with a specific weight near that of fresh water or of sea-water are very few.

(*b*) The buoyancy of seed and fruit has no direct relation to the density of sea-water, and even if the ocean was deprived of all its dissolved salts, the agency of the dispersal of plants by currents would not be materially affected.

(*c*) Small changes in sea-density, such as the physicist would allow, would, therefore, have no appreciable influence on the operations of the currents as plant dispersers; and only great changes in density, such as are presented by the waters of the Dead Sea, would add materially to the number of floating seeds and fruits.

(*d*) Although the specific weight of seeds and fruits in its relation to sea-density may be regarded as an accidental attribute, their non-buoyancy in the great majority of plants has had a far-reaching influence not only on plant-distribution, but on plant-development. The plant-world would be transformed if all seeds and fruits floated in sea-water.

(*e*) If the floating seed or fruit displays a quality that, so far as the density of the sea is concerned, has been developed in quite another connection, we have next to inquire whether the structure of such buoyant seeds and fruits also affords evidence of non-adaptation.

CHAPTER XI

ADAPTATION AND MEANS OF DISPERSAL

Nature has never concerned herself directly with providing means of dispersal.—Fleshy fruits not made to be eaten.—Nor "sticky" seeds to adhere to plumage.—Nor prickly fruits to entangle themselves in fur and feathers.—The dispersal of seeds a blind result of the struggle between the intruding Evolutionary power and the controlling influence of Adaptation.

BEFORE entering into a discussion of the causes of the floating powers of seeds, it is necessary that I should state my general position on the relation between capacities of dispersal in the organic world and the question of adaptation. Adaptation runs through all the organic and inorganic worlds, and we cannot conceive an universe without it. The naturalist who looks only for the end in the purpose served makes but a partially legitimate use of the phrase. On the other hand, it has been improperly appropriated by those who hold to the theory of Natural Selection, as indicating the result of small fortuitous variations that have chanced to be of service to the species in the struggle for existence. There is no question here of any end in view. Nature is represented as working blindly, and the result of such "fortuitous variation" is termed an adaptation. We cannot, however, pick and choose only adaptations that are very evident in their character. We must include everything in the organic world as an adaptation, whether apparent or not, that is in direct relation with the organism's conditions of existence. It is not conceivable that an organism can be adapted to conditions outside its environment, and yet many so-called adaptations are of this character.

Nature—and I here confess my belief in a determining agency working above and through all living and dead matter, but largely controlled and checked by the laws of the physical world—Nature, as I apprehend, has never concerned herself directly with providing

means of dispersal either for plants or animals. With regard to plants, she makes no direct provision for the distribution of their fruits or seeds. If she had done so, she would have employed some uniformity in her methods, as in the instance of the means of reproduction ; whereas the modes of dispersal are almost infinite in their variety. When I say that Nature makes no direct provision for the dispersal of plants and animals, I mean not in the sense that a bird is adapted for an aerial life, or an aquatic plant for a more or less submerged existence. That a bird is often able to distribute its kind over a great area is the "accident" of its conditions of existence. In a similar way the wide distribution of the "ticks" that they carry round the world is due to the parasitical habits of these insects, habits that have been acquired without any view to their mode of dispersal by birds.

Similarly it cannot be said of seeds or fruits that are transported by birds, whether adhering to their plumage by means of hooks or hairs, or through some viscid excretion, or inclosed in soil adhering to the feet or legs, or carried in the stomach and intestines, that Nature has made any special provision for their dispersal. The dispersing agencies take advantage of certain capacities or characters of a seed or fruit that have been developed in the plant for quite other reasons and in conformity with quite other principles. There may be mentioned as examples the mucosity of seeds, the fleshiness of fruits, the occurrence of hairs and prickles, &c. Yet as far as their connection with dispersal is concerned, such capacities and characters are blind results in the history of the plant's development, the dispersing agencies making use of what was not intended for them.

"Adaptation to definite life-purposes," as Sachs terms it (*Physiology of Plants*, 1887, p. 122), is seen everywhere ; but it is adaptation restricted to the organism's conditions of existence. It is not conceivable, as I have said, that an organism can be adapted to conditions outside its environment. If there is such a seeming adaptation, it is but a blind result, the accidental outcome of collision or contact between two sets of conditions. If we represent a number of these sets of conditions by several circles gradually increasing in size until they encroach on each other, we find that the circles lose their form and acquire a polygonal shape. All characters seemingly connected with modes of dispersal have only this indirect relation to such agencies ; and their utility in these respects is an accident in the plant's life. They have not been acquired in connection with the dispersing medium, but are

the products of the laws of growth and heredity, guided by a determining agency, and acting within the organism's conditions of existence. It is within these narrow limits that all evident adaptations lie. In matters outside the conditions of the development of seeds and fruits, the evolutionary or determining principle "lets them go." Detached from the plant, they come in contact with conditions for which they were never created. The predominant power in Nature, that brings to a successful issue the development of an organism, has its limitations, and this is one of them, the evolutionary or determining influence being ever checked and hampered by the laws of the inorganic world.

I can only refer briefly to some of the reasons that have led me to apply this view of the duality of forces in Nature to the subject of plant-dispersal. The principles of evolution and adaptation rule the world except in matters of dispersal. Take, for instance, the fleshy fruits which the gardener often makes more attractive to birds than they are in the wild condition. The result is certainly to increase their facilities for dispersal by birds; but such a result was as little intended by man as it was by Nature when species of Cornus, Ficus, Prunus, Viburnum, and other genera matured their drupes, berries, and fleshy fruits in the Cretaceous epoch.

Children are now taught in several excellent little books on "Nature-Study" that fleshy fruits are specially adapted to be eaten by animals to secure the distribution of the seeds. We read in one book that plants produce these fruits "on purpose to be eaten," in another that they are "intended to be eaten," and in a third that the seed-coverings are adaptations, all with the ulterior object of distribution by frugivorous animals. I must be pardoned if I venture to express my dissent from these statements, more especially since they are made by authors from whom it might be thought almost impertinent for me to differ. Yet authority can be claimed for holding the opposite view.

When the botanist speaks of "useless secretions" in a plant, he is alluding amongst other things to the sugar and organic acids of fruits. "How and why all these substances originate is," as Professor Sachs observed in the work before quoted, "not known." It is, however, suggested by Dr. Kerner, in his *Natural History of Plants* (Engl. edit. i, 460—462), that such secretions, though useless to plants, may exist for the purpose of alluring animals to assist in seed-dispersal. There are some botanists, it may be remarked, that would reject such a view of the nature of fruits. Dr. Stapf in

his memoir on the flora of Kinabalu observes in this connection that the fact that a fruit is fleshy and attractive to birds is "no proof that it is really devoured by them, and still less that it is dispersed by them." Neither in fleshy fruits, nor in minute seeds, nor in seeds capable of being transported by the wind does he regard the general object of the particular character as primarily to act as a means of dispersion.

The same plea is made for the mucosity of seeds like those of Capsella and Plantago (see Note 43), or for the "stickiness" of other seeds and fruits like those of Pisonia, qualities that favour adherence to passing objects. This is the reason, we are told, why seeds are "sticky." Such secretions I infer are often materials lost to the plant; and being in that sense excretory we are not called on to supply a use for them. They can, therefore, not be regarded as having any teleological significance, since adaptation arises only from the requirements of the plant's conditions of existence. If they are serviceable in assisting the distribution of seeds, such an event can only be described as an accident in the plant's life arising from chance contact with another environment.

The appendages of seeds and fruits, such as hooks and hairs, that render them liable to adhere to fur or feathers, are also regarded as special adaptations to this end. Without entering into the physiological significance of hairs and prickles generally, concerning which, as many of my readers will know, much might be said not in favour of such a view, I would refer to cases like that of Cæsalpinia Bonducella, where the large prickly pods could not possibly be intended to aid the plant's dispersal, whilst the leaf-branches are also prickly, and the seeds are well known to be distributed by the currents. There are other cases like that of Bidens cernua where the achenes, by reason of their barbed bristles, and on account of a layer of "buoyant tissue" in the fruit-coats, are dispersed both by birds and by water. We may fitly ask to which capacity the theory of adaptation should be applied. Spiny fruits may be sometimes so large, as in the instance of Trapa natans, that the question of adaptation to dispersal cannot be raised.

The great variety of the modes of dispersal of seeds is in itself an indication that the dispersing agencies avail themselves in a hap-hazard fashion of characters and capacities that have been developed in other connections. Seeds and fruits, having developed certain characters under a particular set of life-conditions, on being detached from the parent plant are brought into contact with conditions quite outside their original environment. Qualities and

capacities are then brought into play which have no connection with the life-history of the plant. The care with which the mother plant guards the maturing seeds, and the protection of the environment, are at a certain period withdrawn, and the seeds are left to take their chance under strange conditions. It would be idle to see anything purposeful in the waste that results. Rather we would see in it the effect of one of the numerous limitations of the determining or evolutionary power in Nature. Such a power has to adapt its workings to the laws of the physical world, checked here, frustrated there, at times, as in this particular case, losing all control, but in the end prevailing.

My general position may be thus summarised. As concerning the distribution of fruits and seeds, the dispersing agencies take advantage of characters and capacities that were never intended for them, characters and qualities indeed that are often only brought out in relation to another environment. Thus no question of adaptation as regards means of dispersal can arise, since such capacities for dispersal have no connection with the plant's life-history. That seeds are dispersed at all is a blind result of the ever-continued struggle between the opposing forces of evolution and adaptation; that is to say, between the determining power that lies behind organic life and the physical conditions to which it has to adapt its ends.

CHAPTER XII

THE CAUSES OF THE BUOYANCY OF SEEDS AND FRUITS OF LITTORAL PLANTS WITH ESPECIAL REFERENCE TO THOSE OF THE PACIFIC ISLANDS

The classification of buoyant seeds and fruits.—The first group, where the cavity of the seed or seedvessel is incompletely filled.—The second group, where the kernel is buoyant.—The third group, where there is air-bearing tissue in the seed-tests or fruit-coats.—The buoyant seeds and seedvessels of the littoral plants of the British flora.—Summary.

IN the following pages I have adopted in its main features the classification of buoyant seeds and fruits employed by Professor Schimper in his work on the strand-flora of the Indo-Malayan region. The causes of buoyancy, as he points out, are very various, but they can be arranged in a few categories; each category, however, usually admitting great variety within its limits. It is this want of uniformity that first attracts our attention when we come to study the structure of seeds and fruits from the standpoint of their buoyancy. Whilst in the Pacific I went over most of the field traversed by Professor Schimper in Malaya (the majority of littoral plants of these regions being common to both), and as a result I have added not a few plants to his original groups.

It will be seen from the following synopsis that there are three principal groups. The first group includes those seeds and fruits where the buoyancy is derived from unfilled space in the seed or fruit cavity. The second group comprises those seeds or fruits where the floating power is due to the buoyant kernel or nucleus. The third group includes those where the buoyancy arises from the existence of air-bearing tissue in the coverings of the seed or fruit.

The first two groups I will term the mechanical or non-adaptive groups, not only on account of the structure inducing the buoyancy,

but because, as Professor Schimper remarks, the same structure often occurs with inland fruits and seeds possessing little or no floating power. In many of these cases, as he points out, the question of adaptation to dispersal by ocean currents cannot, therefore, be raised. The third group may be named the adaptation group, because it is on these examples of buoyant seeds and fruits that this investigator chiefly based his contention that in the main the structures concerned with buoyancy represent adaptations to dispersal by currents effected through the agency of Natural Selection. It is accordingly to this group that Professor Schimper especially directed his attention, and the result of his observations made in the home of the plants and of his investigations in the laboratory has been the elucidation of many difficult points in the structure of their fruits and seeds. To the two "mechanical" groups he did not pay the same attention; and as their examination came more within the limits of my own capacity as an inquirer I have worked them out with some detail, the subdivisions of the first group being my own as well as much of the material.

Synopsis of the buoyant fruits and seeds of littoral plants of the tropical Pacific classified according to the cause of buoyancy. (The authorities are indicated by the initial letter, S = Schimper, G = Guppy. Details are given under some of the species in latter part of volume.)

FIRST GROUP.—The floating power is derived from unoccupied space in the cavity of the seed or fruit, no part of the seed or fruit as a rule possessing independent floating power.

SUB-GROUP I., where the seed is concerned.

SECTION I. The seeds have little or no albumen, and neither the tests nor the seed-contents have any buoyancy. The cotyledons are generally large, foliaceous, and crumpled or folded, or otherwise arranged, so that the seed-cavity is incompletely filled.

S. G. Hibiscus tiliaceus.
G. Hibiscus diversifolius.
S. G. Thespesia populnea.
S. Suriana maritima.
G. Kleinhovia hospita, *variable.*
S. G. Colubrina asiatica.

S. Dodonæa viscosa.
G. Argyreia tiliæfolia, *variable*.
G. Ipomea bona nox, *variable*.
G. Ipomea glaberrima, Boj.
S. G. Ipomea grandiflora.
S. G. Ipomea pes capræ.
G. Ipomea turpethum, *variable*.
G. Cassytha filiformis.
S. Euphorbia atoto.

Notes.—The species marked "variable" have seeds that sometimes sink and sometimes float. With the exception of Kleinhovia they are only at times littoral in station.

The plants of the British flora are represented by Convolvulus soldanella and C. sepium, the last being "variable" and not a littoral species.

SECTION II. All the seeds belong to the Leguminosæ. Neither the tests nor the seed-contents have any buoyancy, the floating power arising from a large central cavity produced by the bending outward of the cotyledons during the final shrinking stage of the maturation of the seed.

S. Mucuna (generically).
G. Mucuna urens D.C. (Hawaii).
G. Mucuna, species of.
S. G. Vigna lutea.
S. G. Cæsalpinia bonducella.
G. Cæsalpinia bonduc.
G. Entada scandens.

SUB-GROUP II., where the fruit is concerned.

SECTION III. The seed only partially fills the fruit-cavity, and as a rule is not buoyant. The fruit shell, usually woody, may be also buoyant.

S. G. Heritiera littoralis.
G. Smythea pacifica.
G. Dalbergia monosperma.
S. G. Derris uliginosa.
S. G. Pongamia glabra.
G. Desmodium umbellatum.
G. Gyrocarpus jacquini.

SECTION IV. The floating power is derived from empty seed-cavities, where owing to abortion of the ovule or some similar cause the seed is not developed.

S. G. Morinda citrifolia.
G. Premna tahitensis.

Note.—Professor Schimper, in the case of Morinda citrifolia, holds the view that we have here a special adaptation to dispersal by currents.

SECOND GROUP.—Here the floating power is due mainly or entirely to buoyant kernels. In the case of seeds the tests are non-buoyant; but with "stones" the floating capacity may be aided by a layer of air-bearing tissue inside the shell.

SECTION I. Non-Leguminous.

S. G. Ximenia americana (drupe).
S. G. Calophyllum inophyllum (drupe).

Note.—Professor Schimper would place these two plants in the second section of the third group on account of the layer of air-bearing tissue inside the shell of the "stone"; but they are assigned to this section, since the floating power is mainly due to the buoyant kernel.

Arenaria (Honckeneya) peploides, a British beach plant, belongs here.

SECTION II. Leguminous seeds.

G. Dioclea.
G. Strongylodon lucidum.
S. Canavalia (generic).
G. Canavalia sericea.
S. G. Canavalia obtusifolia.
S. Erythrina (generic).
S. G. Erythrina indica.
P. Erythrina ovalifolia (Penzig).
S. G. Sophora tomentosa.
G. Afzelia bijuga.
G. Lathyrus?

THIRD GROUP.—The floating power is due to the presence of air-bearing tissue in the seed-tests or fruit-coats.

SECTION I. The buoyant tissue occurs at the outside or forms the periphery of the seed or fruit. Unless otherwise indicated the fruit is implied in the list below.

S. G. Carapa moluccensis (seed).
S. G. Carapa obovata (seed).
G. Inocarpus edulis.
G. Serianthes myriadenia.
G. Parinarium laurinum.
S. G. Barringtonia speciosa.
G. Barringtonia racemosa.
S. G. Pemphis acidula (seed).
S. Terminalia (generic).
S. G. Terminalia katappa.
G. Terminalia litorea.
S. Lumnitzera (generic).
S. G. Lumnitzera coccinea.
S. G. Guettarda speciosa.
G. Wedelia strigulosa.
S. G. Scævola Kœnigii.
S. G. Cerbera Odollam.
G. Ochrosia parviflora.
S. G. Cordia subcordata.
S. G. Tournefortia argentea.
S. G. Clerodendron inerme.
G. Vitex trifolia.
G. Vitex trifolia, var. unifoliolata.
G. Tacca pinnatifida (seed).
S. Nipa fruticans.
S. Cocos nucifera.
G. Scirpodendron costatum.

Additions of shore-plants from Malaya and tropical America mostly given in Schimper's work on the Indo-Malayan strand-flora.

S. Cynometra cauliflora.
S. Conocarpus erectus.
S. G. Laguncularia racemosa.
S. Lumnitzera racemosa.
S. Sonneratia (seed).
S. Barringtonia excelsa.

S. Scyphiphora hydrophyllacea.
S. Wollastonia glabrata.
G. Hippomane mancinella.

Note.—Here belong a species of Vitex, probably V. agnus castus, the fruits of which occur in the stranded drift of the Sicilian beaches, and also the British littoral shore-plants, Cakile maritima, Crithmum maritimum, Matricaria inodora, and Scirpus maritimus.

SECTION II. The buoyant tissue forms a layer inside the hard test of a seed or inside the shell of he "stone" of a drupaceous fruit, and to this cause the floating power is mainly or entirely due.

G. Mucuna gigantea (seed).
S. Hernandia peltata.
S. Excæcaria agallocha.
S. Cycas circinalis.
S. Pandanus odoratissimus.
G. Anona paludosa (seed) of tropical America.

Note.—I have followed Schimper in respect to Pandanus, but it might be by some placed in the first section of this group.

Here belongs Euphorbia paralias, a British littoral plant, the buoyant seeds of which occur in the stranded seed-drift of English and Mediterranean beaches.

In the following general discussion of the groups, reference will be made only to the plants best illustrating the different varieties of structure connected with buoyancy; whilst mention of the other plants will in some cases be found in other parts of this volume, as shown in the Index; and the matter is discussed at some length in not a few of the species.

THE FIRST GROUP.

Of the first group, where the floating power is due to the unoccupied space in the cavity of the seed or fruit, the Convolvulaceæ offer the most typical examples. Here as a rule the crumpled embryo fills the seed-cavity more or less incompletely; and it is on the relative size of the unoccupied space that the sinking or floating of the seed depends. In those plants where the seed sinks the seed-cavity may be almost filled, as in Ipomea tuberculata, or densely packed, as in Ipomea pentaphylla, and

in species of Cuscuta. When the seed floats, as with Ipomea pes capræ, I. glaberrima, &c., the unoccupied space is relatively large; and when, as with I. bona nox and I. turpethum, the behaviour of the seeds is irregular, some floating, and others sinking, a corresponding variation exists in the extent to which the seed-cavity is filled. This applies also to the irregular behaviour of the seeds of Ipomea peltata and of Argyreia tiliæfolia. A singular instance is afforded by the seeds of Ipomea insularis, collected by me in Fiji and Hawaii. Those from Fiji were incompletely filled, and consequently buoyant. Those from Hawaii were more densely packed and sank. . . . The three British species of Convolvulus illustrate the same principle, namely, C. arvensis, with non-buoyant seeds; C. soldanella, with buoyant seeds; and C. sepium, with seeds irregular in behaviour.

In the case of plants of the Convolvulaceæ, possessing buoyant seeds, there is always evidence of marked shrinking of the seed-contents before the final setting and hardening of the seed-coats. The embryo often appears shrivelled and dried up, and is almost brittle, so that large spaces are produced in the seed-cavity. If we partly divide such a seed and place it in water, the embryo absorbs water rapidly, and within an hour is soft, healthy-looking, and much swollen, the interspaces being filled with a jelly-like mucilage. It is therefore evident that absolute impermeability of the seed-coats is essential for the successful transport by sea-currents of the floating seed; and we can only suppose that the shrinking of the seed-contents takes place before the final setting of the tests. That with the buoyant seeds the coats are quite waterproof was illustrated in many of my experiments where, after a period of flotation covering several months, and sometimes a year or more, the seed-contents were still quite dry and shrunken. The limit of buoyancy, as I have shown in Chapter IX., depends on an attempt at germination on the part of the floating seed, which then absorbs water, softens, swells, and sinks.

It is, therefore, not a matter of surprise that non-buoyant seeds of the Convolvulaceæ do not gain floating power after prolonged drying of many months. It is also to be expected that, as we find in Fiji, when a characteristic shore-species with buoyant seeds like Ipomea pes capræ extends far inland, the seeds retain their floating powers. Seed-buoyancy of this description is, on the face of it, purely mechanical.

Another type of the buoyant seeds of the first group is

EXPLANATION OF THE DIAGRAMS ILLUSTRATING THE CAUSES OF SEED-BUOYANCY

1. *Entada scandens* (natural size): (*a*), the shell; (*b*), the kernel; (*c*), the inter-cotyledonary cavity. The shell consists of three coats—an outer and an inner hard chitinous coat, and an intermediate layer of brown cellular tissue containing little or no air. The buoyancy is due entirely to the central cavity, neither the seed-tests nor the seed contents possessing any floating power (see page 181).

2. *Mucuna urens*, from Hawaii (natural size). The kernel (*b*) sinks, and the shell has no floating power except where it possesses (under the raphe) a layer of dark brown, air-bearing, spongy tissue (*a*). This, however, is not sufficiently developed to endow the seed with buoyancy, which is due to the intercotyledonary cavity (*c*). (see page 111).

3. 4. *Mucuna gigantea*, from Fiji (natural size). The kernel (*b*) sinks, and the seed owes its floating power entirely to the existence in the shell (*a*) of a layer of brown, spongy, air-bearing tissue which is mostly developed at the circumference and is almost wanting at the flat sides of the seed (see page 115).

5. 6. *Dioclea* (*violacea ?*), from Fiji (natural size). Here the kernel (*b*) is buoyant and endows the seed with floating power. Though the shell (*a*) possesses a thick layer of reddish-brown cellular tissue, this tissue contains but little air and aids the floating power but slightly (see page 113).

7. *Strongylodon lucidum*, from Fiji (natural size). The floating power is due entirely to the buoyant kernel (*b*). There is a very scanty amount of loose brown tissue (*a*) under the raphe; but it has no appreciable effect on the buoyancy (see page 113).

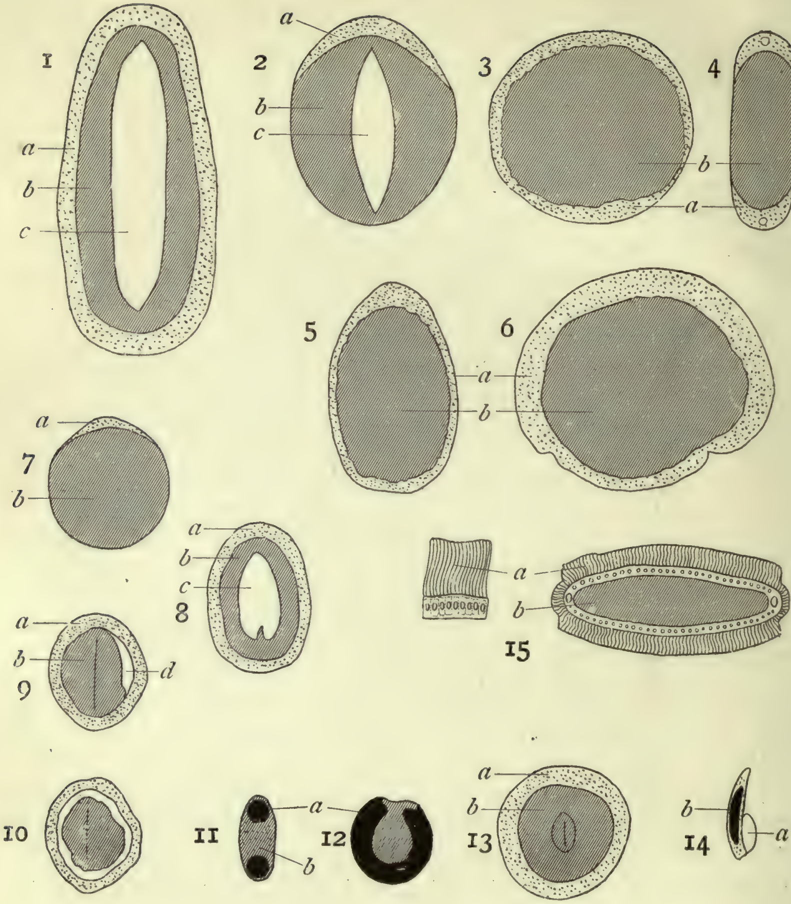
8. 9. 10. *Cæsalpinia bonducella* and *C. bonduc*, from Fiji (natural size). Neither the seed-tests (*a*) nor the kernel (*b*) have any floating power in themselves, the buoyancy being connected with a large internal cavity (*c*), which normally is intercotyledonary, as in Fig. 8 (C. bonducella). With both plants, but more especially with C. bonduc (Figs. 9 and 10), there may be a lateral cavity (*d*), or the kernel may be loose in the shell (Fig. 10), but this does not necessarily imply buoyancy (see page 194).

11. 12. *Arenaria peploides* (enlarged: seeds 4 mm. in size). Here the curved embryo (*a*) sinks, and the spongy air-bearing albumen (*b*) gives buoyancy to the seed (see page 116).

13. *Euphorbia paralias* (enlarged: seeds 3 mm. in size). The kernel (*b*) sinks, and the seed owes its buoyancy to a layer of air-bearing tissue (*a*) in the shell (see page 116).

14. *Morinda citrifolia* (enlarged pyrene 7 mm. long). The floating power is due to the bladder-like air cavity (*a*). The seed (*b*) proper is enclosed in the woody tissue behind the bladder (see page 112).

15. *Cucurbita* (seed enlarged), from the Valparaiso beach-drift (see page 125). The kernel (*b*) has no buoyancy. The shell (*a*) is formed of two layers of air-bearing tissue, the outer composed of prismatic cells and the inner of a spongy vacuola-material.



Diagrams illustrating some of the causes of seed-buoyancy.

presented by several species of Leguminosæ, as with Entada scandens, some species of Mucuna, and Cæsalpinia bonducella. As with the Convolvulaceous seed, the embryo sinks and the seed-shell has no buoyancy; but here the floating power is due to the existence of a more or less symmetrical long central cavity produced by the arching or bending outwards of the large cotyledons which lie usually in close contact with the seed-shell. This arching outward of the cotyledons depends on a shrinking process in the setting or final stage of the maturation of the seed. The stages of the process may be traced in the immature seeds, which are much larger and in some cases twice the size of the mature seed. In this immature condition the seed-coats are soft, and the flabby fleshy and thick cotyledons fill up the seed-cavity. As the hardening and setting process continues, the cotyledons diminish in size, become firmer, and gradually bend outward, leaving a central cavity. This arching outwards is no doubt in part the result of the contraction of the seed-tests during the shrinking process. Considerable variation prevails in the results, and where the cavity is very small the seed sinks. Further details relating to this subject will be given in my treatment of some of the plants, and especially under Cæsalpinia. But it may be here remarked with reference to Hawaiian seeds of Mucuna urens D.C., that although they are strictly referable to this group, they display beneath the hard test, on the side beneath the raphe, a scanty layer of dark spongy air-bearing tissue which is sufficiently buoyant to float up detached portions of the test, but does not of itself give buoyancy to the seed. The significance of this structure will be subsequently pointed out. The seed owes its floating power to the large central cavity, but this layer of spongy tissue adds to its buoyancy.

The section where the buoyancy of the fruit is connected with unoccupied space in the fruit-cavity is extremely heterogeneous in its composition. Every fruit has a method of its own, and the great variety of causes of buoyancy of a mechanical character is here exemplified. For instance, with Gyrocarpus jacquini and Cassytha filiformis the cause of buoyancy is in the main the same as that described in the case of the Convolvulaceæ. The origin of the floating power of the pods of Derris uliginosa is two-fold. In the first place the seed or seeds but partly fill the pod, and in the second place the seed is able to float of itself by reason of its possessing, as in the seeds of Entada scandens, a large central cavity produced by the arching out of the cotyledons during the

final stage of maturation. A double cause is also to be assigned to the buoyancy of the fruits of Heritiera littoralis and of Smythea pacifica, where, in addition to the unoccupied space produced by the shrinking of the seed, the fruit-case itself floats, though nothing but a mechanical explanation is to be given of the floating of empty ligneous fruits.

One of the most suggestive types of buoyancy belonging to the first group is presented by those cases, which are, however, not very frequent, where the floating power is to be attributed to empty seed-cavities produced by the abortion of the ovule or failure of the development of the seed. A significant instance of this is afforded by the fruits of Premna taitensis, a coast plant. The buoyant "stone" of the drupe, which is often found afloat in the Rewa estuary in Fiji, is 4-locular, each cell containing normally one seed, but as a rule only one cavity contains a mature seed, the three other cavities becoming more or less empty through the failure of their seeds. It can be proved that neither the seeds nor the substance of the "stone" are buoyant, and that the "stone" owes its capacity of floating for months to the empty cavities arising from the failure in development of three out of the four seeds. In Fiji we see the rivers distributing these small fruits, and we find the "stones" stranded on the beaches and floating in the currents amongst the islands; and there can be no doubt that this is one of the effective modes of dispersal of the species; yet, if there was ever a case of accidental buoyancy concerned with dispersal by currents, we have it here. Further details are given in Note 32.

It is probably also to the abortion of the ovule, or to the failure of the seed, that the remarkable air-cavity (see Note 8) to which the pyrenes of Morinda citrifolia owe their floating power, is to be attributed. To this structure Professor Schimper (pp. 165, 183, 200) attaches considerable importance as an example of special adaptation to dispersal by currents through the influence of Natural Selection. He suggests, however, that possibly its morphological significance may be found in its being a peculiarly modified seed-chamber. The case of Premna taitensis above cited indicates that the latter view is the most probable. The subject awaits a careful microscopical study of the seed-development of the genus Morinda since, as elsewhere remarked, the non-buoyant pyrenes of inland species have not such an air-chamber. An outline sketch of a pyrene of Morinda citrifolia is given in the preceding plate. A good figure of it occurs in Schimper's *Plant*

Geography, p. 28. A very suggestive instance of this nature is described under Brackenridgea in Note 46 and in Chapter XIII.

The Second Group.

Here are included those seeds and stone-fruits that possess buoyant kernels. Professor Schimper points out that since this is a feature both with inland as well as coast plants such a character cannot be viewed as an adaptation to dispersal by currents. The plants concerned belong mostly to the Leguminosæ, and we find here some of the most widely spread of strand species, such as Canavalia obtusifolia and Sophora tomentosa, as well as some of the giant climbers of the coast forests belonging to the genera Dioclea and Strongylodon. The kernels when divested of their coverings float buoyantly, but they soon absorb water and sink usually in a day or two, a circumstance indicating that it is to the impervious coverings that they indirectly owe their capacity to keep the seed or fruit afloat. It is noteworthy that seeds of Strongylodon lucidum from Fiji display beneath the raphe a trace of an internal layer of loose cellular tissue which, however, has no appreciable effect on the buoyancy; whilst with seeds of Dioclea (violacea ?) from the same locality there is a thick layer of loose tissue which aids the floating power of the kernel but is not of itself sufficiently aeriferous to buoy up the seed.

This leads one to refer to two other plants belonging to this group, Calophyllum inophyllum (Guttiferæ) and Ximenia americana (Olacineæ), where, though the floating power is mainly due to the buoyant kernel, it is also aided by a layer of air-bearing tissue inside the hard shell of the "stone" of the drupe. Professor Schimper places these fruits in the third or adaptive group on account of the layer of buoyant tissue, but it would be more correct to class them according to the predominant cause of their buoyancy. It can be shown that with a non-buoyant kernel the "stone" no longer floats. This double cause of the floating power renders an explanation very difficult, since it would seem indefensible to give conflicting interpretations of their nature. With Ximenia americana there is another great difficulty. Its drupes are known to be dispersed by fruit-pigeons (*Introd. Chall. Bot.*, p. 46); and judging from the rare occurrence of the "stones" in the drift there is good reason to believe that bird agency in the Western Pacific is predominant in the dispersal of the plant. It is by such test cases as this that we must put to the proof the reality or non-reality of the influence of adaptation on seed-buoyancy.

The Third Group.

We have here those plants where the floating-power is entirely or mainly due to an air-bearing tissue in the seed-tests or fruit-coats. Several of the fruits are figured in Schimper's *Indo-malayische Strand-flora*, and one or two are figured in the English edition of his work on *Plant-Geography*, p. 29.

In the first section, where the buoyant tissue occurs at the outside or forms the periphery of the seed or fruit, are included several of the most familiar of the littoral trees and shrubs of the Pacific islands, such as Barringtonia speciosa, Cerbera Odollam, Guettarda speciosa, Pemphis acidula, Scævola Kœnigii, Terminalia katappa, and several others named in the synopsis. I cannot enter into detail here, but the reader will find fuller particulars of each plant in most cases in Professor Schimper's work, and in some instances in my separate discussion of the plants concerned. In nearly all cases we are concerned here with the fruits, and only in a few cases with the seeds, as with Carapa and Pemphis acidula.

This investigator observes that to this sub-group belong the fruits and seeds usually described in systematic works as provided with corky or suberous coverings; but he points out (p. 167) that the resemblance is nearly always quite superficial, and is limited to colour and consistence, suberous tissue occurring in only a few cases, as in the fruit-coats of Clerodendron inerme. The buoyant tissues, he remarks, are often more or less ligneous, and in those cases where there is no lignin reaction they resist the action of sulphuric acid much more effectively than pure cellulose; whilst in their physical characters, as well as in their behaviour with reagents, they differ just as much from ordinary cork. Thus, they are but little elastic and often easily crumble away; whilst in large fruits, like those of Cerbera and Terminalia, they would soon be stripped off entirely when subjected to the "wear-and-tear" of transport by currents, if they were not traversed by numbers of stout, tough fibres which hold the materials together. Where the buoyant tissues are firmer, as with Clerodendron inerme and Cordia subcordata, the fibrous framework is scanty or absent, whilst very small seeds or fruits, like those of Tournefortia argentea and Pemphis acidula, where the "wear-and-tear" would be comparatively slight, often possess no protecting fibres in the buoyant tissues.

In one or two fruits, like those of Cerbera Odollam, these tissues display large intercellular spaces; but in the majority of

cases such spaces are insignificant in size or absent altogether. Speaking generally, however, there is, as Professor Schimper observes, great similarity in the structure of the buoyant tissue in the coverings of these fruits and seeds. The cell-walls are thin or only slightly thickened, and detached air-bearing portions of the tissue will float for many weeks. The great floating capacity of these fruits and seeds is stated by this investigator to be entirely due to the tenacity with which the air is retained in the covering tissues. It is, however, noteworthy that in the case of Scævola Kœnigii the fruits are just as well suited for dispersal by frugivorous birds as by the currents, a significant circumstance discussed in the next chapter.

The second section contains those plants where the buoyant tissue occurs inside the hard shell of the fruit or seed, such as is found, for example, in Anona paludosa, Mucuna gigantea, Hernandia peltata, Cycas circinalis, &c. Professor Schimper here includes Calophyllum inophyllum and Ximenia americana; but I have before remarked that the buoyancy of their fruits is mainly due to their buoyant kernels. This aeriferous tissue forms a layer between the seed or nucleus and the hard outer shell. It is described by the above-named authority as soft or friable and dark brown. The cells contain air and may be closely arranged or separated by small interspaces, their walls being neither woody nor suberous.

The structure of the buoyant seeds and seedvessels of the littoral plants of the British flora.

The littoral plants with floating seeds or fruits form but a section of the strand-plants of the British flora, scarcely a third, as is pointed out in Chapter IV., of the total number. Though small in number they exhibit great variety in structure; and notwithstanding that as far as they have been examined they may all be referred to one or other of the groups and sections of the classification adopted in the synopsis for the plants of the Pacific islands, nearly every plant presents in the structure of its seeds or seedvessels a type of buoyant structure different from the others.

The first group is represented by the seeds of Convolvulus soldanella, which owe their floating power to the incomplete filling of the seed-cavity. The second group, where the buoyancy arises from the buoyancy of the kernel or nucleus, is illustrated by the

I 2

seeds of Arenaria (Honckeneya) peploides, but in a fashion quite unique. The test is thin but impervious, and has no buoyancy; the curved embryo also sinks; and the floating power arises from the air contained in the loose spongy albumen, around which the embryo is coiled (see figure). A more normal component of the second group is represented in some Leguminous seeds, perhaps of Lathyrus maritimus, that occur regularly amongst the stranded seed-drift of the north coast of Devon. Here the kernel of the seed is buoyant. The seeds of Euphorbia paralias are indebted for their floating capacity to a layer of spongy tissue containing large air-spaces placed between the kernel and the chitinous outer test, neither of which possess any floating power (see figure). They thus belong to the second section of the third group.

The fruits of Cakile maritima, Crithmum maritimum, Matricaria inodora, and Scirpus maritimus, all belong to the first subdivision of the third group where the air-bearing tissue exists in the peripheral coverings, the seed or nucleus in all cases sinking. With Cakile maritima there is a light spongy outer case of aeriferous tissue, which, however, soon loses the epidermis, a circumstance that probably explains the limited period of flotation of about a week. The walls of the mericarp of Crithmum maritimum are composed of spongy cellular air-bearing tissue with a persistent epidermis, and the floating powers of the fruits are consequently great. The achenes of Matricaria inodora have beneath the epidermis a layer of buoyant tissue, and their structure is similar to that found with the buoyant achenes of littoral species of Wedelia, plants of the same order of Compositæ that are found on the Pacific islands. The cause of the floating power of the fruits of Scirpus maritimus lies entirely, according to Kolpin Ravn, in the air-bearing cells of the epidermis. The reader will find the results of my experiments on the buoyancy of the seeds in Notes 16, 17, and 18.

Summary of the Chapter.

(1) Following the main lines of Schimper's classification of those of the Indo-Malayan region which possesses for the most part the same species, the buoyant seeds and fruits of the littoral plants of the Pacific islands are classed in three groups: the *first* where the cavity of the seed or fruit is incompletely filled, the floating power arising from the empty space; the *second* where the

buoyancy is derived from the buoyant nucleus or kernel ; and the *third* where it arises from air-bearing tissues in the coats of the seed or fruit.

(2) The first and second groups, in which the question of adaptation to distribution by currents through the agency of Natural Selection is not raised, since the same structural characters are found in seeds and fruits of inland plants not dispersed by the currents, are termed the mechanical or non-adaptive groups. The third is distinguished as the adaptive group, because it is here that Schimper finds evidence in favour of the Selection Theory.

(3) The first group is best represented by the Convolvulaceous and the Leguminous types. In the former, which is well illustrated by Ipomea pes capræ, the seed-cavity is imperfectly filled by the crumpled embryo, the result of the shrinking process during the final setting of the seed. In the latter, which is exemplified by Entada scandens and Cæsalpinia bonducella, the seed displays a large central cavity produced by the arching outward of the cotyledons during the shrinking process accompanying the last stage of the maturation of the seed. As an instance of fruits belonging to the group, those of Heritiera littoralis may be cited. An uncommon type is presented in the "stones" of the drupes of Premna taitensis, and in the pyrenes of Morinda citrifolia, where the buoyancy arises from empty seed-cavities resulting from the failure of some of the seeds.

(4) The second group with buoyant kernels includes mostly widespread Leguminous species, such as Canavalia obtusifolia and Sophora tomentosa.

(5) The third or "adaptive" group comprises many of the characteristic littoral trees and shrubs of the Pacific islands, such as Barringtonia speciosa, Guettarda speciosa, Terminalia katappa, Tournefortia argentea, &c., that contain in their fruit-coverings a buoyant cork-like material often bound together by fibres, but which proves on examination to resemble cork only in appearance. In another type, illustrated by the fruits of Cycas circinalis and the seeds of Anona paludosa, the buoyant tissue forms a layer inside the shell of the seed or "stone."

(6) Some fruits like those of Ximenia americana and Calophyllum inophyllum illustrate both the so-called mechanical and adaptive principles in their structure ; whilst with the first-named species they are as well adapted for dispersal by frugivorous birds and are known to be a favourite food of fruit-pigeons. The same difficulty arises with the fruits of some other characteristic littoral

plants, as with Scævola Kœnigii, the drupes of which are equally well fitted for dispersal by birds and currents.

(7) The same general principles have been at work in determining the structures concerned with the buoyancy of the fruits and seeds of British littoral plants. Although the species are few in number they exhibit in this respect great variety, eight species illustrating six or seven types of buoyant structure.

CHAPTER XIII

ADAPTATION AND SEED-BUOYANCY

The question of the operation of Natural Selection.—Are there two principles at work?—The presence of buoyant tissue in the seed-tests and fruit-coats of inland plants, both wild and cultivated.—Useless buoyancy.—The buoyancy of seeds and fruits is not concerned with adaptation.—Summary.

WHEN we speak of a certain structure as an adaptation to dispersal by currents through the agency of Natural Selection, it is necessary at the outset to be quite clear as to what is implied. Professor Schimper, who brought his great and varied knowledge of many other phases of plant-life to bear on this subject, is careful to clear the ground of preliminary erroneous conceptions in such a perspicuous and impartial manner that we cannot do better than follow his guidance. There are, he observes (p. 178), many mechanisms or contrivances in plants, which, though they seem to have arisen with a fixed purpose, can in no wise be regarded as having been developed for that end, since they were produced in quite a different connection and have merely acquired a new or supplementary function, of which they are the cause and not the effect.

This is very much the position that I have taken up for the whole subject of the relation between plants and their dispersing agencies, and it will be found discussed in Chapter XI. It involves, as I venture to think, a dominant principle in the organic world, which it is one of the objects of this work to emphasise, namely, that Nature in dispersing plants habitually makes use of structures and capacities that were originally developed in quite another connection. Behind this change of function, this new purpose, lies the secret of the organic world. There is for me no more pregnant fact in plant-life than the thistle-seed blown before the wind, or the seed of our sea-convolvulus floating in the sea. It proves to my mind that the evolutionary power in nature is checked and

hampered by conditions not of its own creation, and that two opposing forces are ever at work, the one creating and the other limiting the creative power, the actual mode of dispersal being but a blind and accidental result of the struggle.

The question of the operation of Natural Selection is not raised, as Professor Schimper indicates, until we consider whether the new function has had any bettering influence on the structure or mechanism with which it has come to be concerned. If such a modification is thus brought about it might be legitimately claimed as a result of this agency, and the term "adaptation" could be used. But if there is no evident change produced, we should be compelled to assign very subordinate limits to the capacity of Natural Selection; and in the instance of buoyant fruits and seeds it would be restricted to determining a plant's station by the water-side and in increasing its area. It is only in the first case that we could speak of them as adaptations in the meaning attached to this term in the language of the Selection Theory. It would at first sight seem easy to ascertain whether the characters of fruits and seeds, to which the buoyancy is due, are adaptations in this sense of the word; but in reality it is far from being so. We can, however, proceed with unanimity up to a certain stage in the argument; but there agreement ends.

It has been before established that in the Pacific islands, and indeed in the tropics generally, the plants with buoyant seeds or seedvessels are mainly stationed at the coast. It has also already been shown that this littoral station is often associated with a special buoyant-tissue in the coverings of the seed or fruit; and it will now be pointed out that this tissue is, as a rule, absent or but scantily developed in the case of inland species of the same genus. Of great importance, remarks Professor Schimper (p. 179), in relation to the Selection Theory and the development of adaptations, is the comparison of the fruits and seeds of strand-plants with those of allied inland species; and he finds here evidence in support of the Darwinian view. He takes the cases of the genera Terminalia and Calophyllum, which contain both inland and littoral species; and he shows that although the same buoyant-tissue occurs in the fruit-coats of inland species, it is there much diminished, and in consequence the floating powers are considerably lessened or lost altogether (see Chapter II.). It is not pretended that this tissue has had any connection in its origin with dispersal by currents, but merely that its greater development in the shore species is an adaptation to this mode of transport.

Further testimony is adduced by this investigator (p. 182) in supporting his view in the fruits of the genera Barringtonia, Clerodendron, Cordia, and Guettarda, where the buoyant tissues extensively developed in the coast species are either non-existent or only represented by a trace in the inland species of the same genus, a difference in structure associated with the loss or great diminution of the floating capacity of the fruits concerned. I have been able to establish other examples in the cases of the genera Scævola and Tacca, which will be found referred to in Chapter II.

Professor Schimper (p. 200) points to the circumstance that the "adaptations" in these fruits all belong to the diagnostic marks of the genera and the species, and contends that these plants abundantly prove the erroneous nature of the contention that Natural Selection could have played no part in the elimination of the strand-flora. My own contention is that Natural Selection has played such a part, but that in doing so it has merely availed itself of characters previously existing, without originating, modifying, or improving them in any way. The foregoing evidence might with equal fitness be employed to show, as pointed out in Chapter II., that in the course of ages there has been a great sorting process by which, excluding the mangroves, plants of the xerophilous habit possessing buoyant seeds and fruits have been sorted out and placed at the coast. Direct evidence does not lead us farther than to the establishment of a littoral station for plants thus endowed. The problem whether the characters of their fruits and seeds that are concerned with buoyancy may be regarded as adaptive in the Darwinian sense lies beyond the reach of direct testimony. We can, however, approach it from the outside by several directions, and from some of these we will now proceed to deal with it.

There is first the singular circumstance that in Fiji, when the littoral plants with buoyant seeds or fruits leave the beach and extend far inland, they, as a rule, retain their floating powers and, of course, their buoyant structures. I found this to be true of Cassytha filiformis, Cerbera Odollam, Ipomea pes capræ, Morinda citrifolia, Scævola Kœnigii, and one or two other plants mentioned in Note 44, where this subject is discussed. My experiments on these plants indicated that their fruits or seeds floated equally long, whether obtained from coast or from inland plants. This, at first sight, appears to present a serious objection to the adaptation theory; but it was not so regarded by Professor Schimper, who in a letter to me, dated March 8th, 1900, observed that he did not see "why littoral plants growing inland should lose

their adaptations to littoral life, especially if those adaptations are not conflicting with the conditions of life beyond the littoral zone, and if the competition does not require special adaptations."

My view, however, is that any process of adaptation is unnecessary. All these plants, it is contended, were originally inland plants that acquired the buoyant qualities of their seeds and fruits in the inland stations, and ultimately found a station at the coast through the sorting process above referred to. In the case of plants like Ipomea pes capræ and Cassytha filiformis this would be conceded, since they belong to the acknowledged non-adaptive groups discussed in the preceding chapter. It is only to some of these plants, such as Scævola Kœnigii and Cerbera Odollam, that the adaptation view of Professor Schimper is applied; and the question arises whether we are justified in making such a distinction, or, in other words, whether it is antecedently probable that two independent principles have been at work in determining the fitness of seeds and fruits for dispersal by the currents.

The plants for which the influence of adaptation through Natural Selection is claimed belong, as stated in Chapter XII., almost entirely to the third group. It is admitted that with the other two groups the utmost that any sorting or selecting process would effect would be to determine a station at the coast and to extend the area of distribution. The numerical aspect of the question therefore acquires some importance; and the reader's attention is accordingly directed to the results tabulated in Note 45, where it is shown (assuming for the time that there is no difference of opinion about the adaptive significance of the seeds and fruits concerned) that the plants of the third or adaptive group make up only about half the total. It would therefore appear that if the agencies of Natural Selection have been at work here either in bettering or in developing buoyant structures, half of the shore-plants with buoyant seeds or fruits have not come within their influence.

But the subject takes another aspect when we reflect that in some buoyant fruits, as with Ximenia americana and Calophyllum inophyllum, the two principles would seem to have been at work. Whilst from this standpoint Natural Selection is regarded as having either developed or increased in amount the layer of buoyant tissue in the fruit-coats, the buoyant kernels are not viewed as adaptive in their origin. In the case of Ximenia americana the dispersing agency of frugivorous birds adds another factor, since, as before stated, its drupes are known to be dispersed by fruit-pigeons. In the cases of Scævola Kœnigii and of Vitex trifolia,

two plants belonging to the adaptive group, Professor Schimper (pp. 156, 188) admits also the dispersing agency of frugivorous birds, and he claims it for Morinda citrifolia, in the pyrenes of which he also detects a special adaptation to dispersal by currents. It may be added that, as he also points out, fruits of the non-adaptive group of littoral plants, such as Premna integrifolia (P. taitensis) and Cassytha filiformis, would sometimes also attract birds. In fact, those of the last-named have been found in the crops of pigeons (*Introd. Chall. Bot.*, p. 46).

Looking at all these littoral plants with fruits that are equally fitted for dispersal by birds and by currents, we may now ask, Where does the general principle of adaptation to dispersal lie? Whatever view we adopt, we must apply the same view to all, whether it be a question of dispersal by birds or by currents. We cannot choose between two sets of principles determining the buoyancy of seeds and fruits any more than we can regard a fleshy drupe and a buoyant seed as illustrating different principles regulating the dispersal of plants. Nature works with uniformity in these matters, and if the Natural Selection theory is held to explain one case it ought to account for all. Yet nobody would go so far as this; and this view of dispersal is on many grounds antecedently improbable. These difficulties disappear if we assume that in all cases the dispersing agencies have without modification made use of characters and capacities that were developed, as we now see them, in quite other connections and under quite other conditions.

It will now be necessary to look a little closer into the subject of the buoyant tissue, to the existence of which in their coats about half of the littoral plants concerned owe the floating power of their fruits or seeds. In the first place, it is to be remarked that in the case of some of the seeds of the plants of the non-adaptive groups it is also represented to a small degree in the seed-coats, although, as with Strongylodon lucidum and Mucuna urens, it is not present in sufficient amount to float the seed. In the next place, it should be noted that with some genera possessing, like Terminalia, both inland and coast species it is to be found alike in the fruit-coverings of inland and of littoral plants, though in a less degree in the case of the fruits of inland species, the floating power of which is proportionately diminished. There are, however, a few cases where this buoyant tissue is developed in inland species which belong to genera or subgenera that have no littoral species. This is what we would expect, if Natural Selection has merely

concerned itself with placing plants of xerophilous habit possessing buoyant seeds or fruits at the coast. Under such conditions we would now and then expect to find an inland plant possessing buoyant fruits or seeds of this description that has never been able to establish itself at the coast.

A good instance is afforded by Pritchardia Gaudichaudii, a fan palm peculiar to Hawaii, the drupes of which float for several weeks and have a covering of spongy buoyant tissue (see Chapter XXV.). The seeds of Hibiscus Abelmoschus, a species distinguished subgenerically from the littoral Hibiscus tiliaceus, offer another example. They float for months, and owe their buoyancy to a layer of air-bearing tissue between the kernel and the test, in this respect differing from the seeds of the littoral species, where the floating power is due to unoccupied space in the seed-cavity. The buoyancy of the seeds of Hibiscus Abelmoschus thus offers another example of ineffectual floating power, since it is not a littoral plant, is often cultivated, and has accompanied aboriginal man over much of the tropical zone.

A singular instance of the dispersal by currents of an inland plant that occurs both wild and cultivated in tropical America, the West Indies, and on the West Coast of Africa, is afforded by Spondias lutea, Linn., which is referred to at the end of Chapter XXXII. Its "stones," which are provided with a cork-like covering much as we find with those of Cordia subcordata and Guettarda speciosa, possess great buoyancy, and are found in the river and beach drift of those regions with the seeds in a sound condition.

A very remarkable case of ineffectual buoyancy is presented by the seedvessels of Brackenridgea, which have been found floating in the drift off the coast of New Guinea. They owe their floating power to closed cavities which would seem to arise from the failure of one of the seeds or from the abortion of an ovule. But, according to Beccari, their fleshy coverings would aid their dispersal by frugivorous birds; and since the species are all much localised and are rarely littoral in their habit, it is very probable that birds have mainly effected the dispersal of the genus (see Note 46). It has, however, been shown in the previous chapter that Premna taitensis and Morinda citrifolia owe their dispersal by currents to similar cavities in the seeds or "stones."

Amongst the inland plants possessing seeds or fruits that are dispersed by the currents without aiding the distribution of the species may be recognised types of both the adaptive and non-adaptive groups. A singular instance is afforded by the large

seeds almost an inch long of a huge pumpkin (Cucurbita) which, in sound condition, form one of the commonest constituents of the beach drift on the coast of Chile from Valparaiso northward to Iquique. The fruit is commonly eaten by the lower classes. The seeds, which are very buoyant, contain a kernel that does not float, the buoyancy being due to the water-tight coats which, as shown in the plate in Chapter XII., possess well developed air-bearing tissues. It may here be observed that Martins refers to the germination of seeds of Cucurbita pepo after 45 and 93 days' flotation in sea-water.

One sometimes finds buoyant tissue developed in the seeds of bottle-gourds, where it can serve no useful purpose of dispersal. Thus small bottle-gourds, seemingly of the genus Cucurbita rather than of Lagenaria, are to be commonly found afloat in the Guayaquil River and stranded on the Ecuador beaches. They will float for many months, and contain the seeds dried up into a small loose compacted mass in their interior. These seeds, which contain a layer of spongy air-bearing tissue in their coverings, will in several cases float for months. Some that I had been keeping two months afloat in sea-water germinated freely. It is shown in Note 47 that bottle-gourds containing sound seeds are dispersed far and wide by the currents. In some species the seeds are buoyant, and in others they sink in sea-water; but the gourds themselves will float for probably a year or more, and the floating capacity of the seeds when it exists is too insignificant to affect the fruit's buoyancy.

Other instances of the useless buoyancy of fruits of inland plants are afforded by different species of Citrus. In the floating drift of the Fijian rivers the fruits of the wild and indigenous Shaddock (C. decumana) and of an inedible Orange, also wild and indigenous (C. vulgaris?), are at certain times to be found, the latter often in numbers. The first-named floats four to five weeks in sea-water, and the last-named nearly two months, and both are to be observed floating out at sea between the islands. The fruits of the Tahitian Orange, a variety of C. aurantium, floated in sea-water between three and four weeks. The seeds of these and other species of Citrus sank in from a few hours to a day or two. The buoyancy of the fruit depends on the rind—the thicker the rind the greater the floating power. This was not only shown in the length of the period of flotation, but also in the buoyant behaviour of the fruit. With the Tahitian Orange, where the rind is relatively thin, the fruits floated heavily in sea-water and only protruded slightly above the surface. With the Shaddock and

with the other indigenous species of Citrus, the fruits floated lightly and protruded half-way out of the water.

There is nothing trivial in these examples of buoyant fruits. That they have at times aided in the dispersal of the genus, with man's assistance in planting the seeds of the stranded fruits, I cannot doubt; but unaided by man such buoyant capacities would be useless for purposes of effective dispersal by currents. Between the two genera Terminalia and Citrus there is this great distinction, that the former is more or less halophilous, some of its species being at home on the sea-beaches, whilst the latter, as Schimper would term it, is salt-shy, and includes no halophytes or plants of the sea-shore amongst its species. The only effect of buoyancy of the fruits on the distribution of the species of Citrus would be to place them by the side of the river and the pond. This has evidently been its result in the case of the Shaddock in Fiji, where, as Seemann remarks, it often thickly lines the banks of the rivers.

As also indicating that the buoyancy of the seed or fruit would never, apart from the halophilous habit, endow an inland plant with a littoral station, the examples of the Oak (Quercus robur) and of the Hazel (Corylus avellana) may be taken. As shown in Note 48, these fruits acquire floating power by drying, on account of the space formed by the shrinking of the kernel. They occur commonly in beach drift, but rarely in a sound condition; yet experiment has proved that they will sometimes germinate after prolonged sea-water flotation. The fruits of other species of Quercus are also transported in tropical regions by the currents, but never, as far as I could learn, effectively. The Amentaceæ as an order are "salt-shy," and with only a few exceptions shun the sea-beach.

In the great sorting-process, by which xerophytic plants with buoyant seeds or fruits have been placed at the coast, and hygrophytic plants with similar fruits or seeds have been stationed at the riverside or by ponds and lakes, one might expect to find that other influences may have at times been in conflict with the selecting operation here indicated. To this cause may probably be attributed the cases of "useless buoyancy" above referred to. Here we find in some inland plants fruits and seeds with buoyant tissues in their coverings that in the case of littoral plants would have been regarded as the result of adaptation to dispersal by currents. Such cases go to emphasize the conclusion already indicated that these tissues could not have been developed through the agency of Natural Selection. But the great objection against

the application of the Darwinian view to the general subject of the buoyancy of the seeds and fruits of littoral plants lies in the circumstance that quite half of the plants concerned are admitted to be outside the scope of the theory, and that for these another explanation has to be found. I think we may fairly claim that in a matter which finally resolves itself into a question of buoyancy one explanation should cover all. We have thus to decide whether to regard as adaptations to dispersal by currents the structures of the buoyant seeds and fruits of littoral plants ; or whether to hold the view that as far as dispersal by currents is concerned such structures are purely accidental, and that Nature has never directly concerned herself in the matter at all. The first explanation lies under the disadvantage above alluded to, and it remains to be learned whether the second view could be made to cover all cases of dispersal by currents. Further investigation on many points is yet required ; but, apart from the evidence against Natural Selection as the principal agency that has been produced in this chapter, a powerful argument in favour of the view that the buoyancy of seeds and fruits is not concerned with adaptation is, that as a rule the floating capacity of the seed or fruit has no direct relation with the density of sea-water. Generally speaking, as shown in Chapter X., these seeds and fruits are much more buoyant than they need to be, that is to say, if they owe their floating power to adaptation to dispersal by currents. This is quite in accordance with the argument developed in Chapter XI. with regard to the general question of plant-distribution, that dispersing agencies make use of characters and capacities of seeds and fruits that were never intended for them.

Summary of the Chapter.

(1) There are many mechanisms or contrivances in plants that now serve a purpose for which they were not originally developed.

(2) Of this nature, it is contended, is the relation between fruits and seeds and the agencies of dispersal.

(3) If, however, the structure or mechanism is made more effective by the new function, such a modification may be regarded as an "adaptation" in the language of the theory of Natural Selection.

(4) It is held by Professor Schimper that the structures connected with the buoyancy of the fruits or seeds of several tropical littoral plants are, in the above sense, adaptations; and he points to several genera where the buoyant tissues in the coverings of the fruits or seeds of the coast species are scantily represented or absent in the inland species of the same genus, a difference corresponding with the loss or diminution of the floating powers.

(5) This contrast in structure and in floating capacity between the fruits or seeds of inland and coast species of the same genus is beyond dispute, and the author adduces fresh data in support of it.

(6) But he contends that it is not proved that the relatively great development of buoyant tissues in the case of littoral plants is the effect of adaptation; and that if the selecting process had been confined to sorting out the xerophilous plants with buoyant seeds or fruits and to placing them at the coast, the same contrast would have been produced.

(7) In support of this contention he points out that when such littoral plants extend inland the floating capacity and the buoyant tissues are as a rule retained; and that in those exceptional cases where inland plants possess buoyant fruits or seeds these tissues are sometimes well developed under conditions in which they could never aid the plant's dispersal.

(8) But the most serious objection against the adaptation view is that admittedly only about half of the shore-plants with buoyant fruits or seeds come within its scope. Therefore a second explanation has to be framed for the other plants concerned.

(9) As showing the difficulties raised by regarding some of the structures connected with buoyancy as "adaptive" and others as "accidental," it is pointed out that some fruits possess the two kinds of structure. It is also shown that in several cases fruits endowed with buoyant tissues are just as well adapted for dispersal by frugivorous birds; and the instance of Ximenia americana is cited where a drupaceous fruit, known to be dispersed by fruit-pigeons, possesses also in its "stone" both the "adaptive" and "non-adaptive" types of "buoyant structures."

(10) It is urged that whatever is the relation between the buoyancy of the seeds and fruits of shore-plants and dispersal by currents, there has been a uniform principle affecting all.

(11) The weight of evidence is regarded as adverse to the Natural Selection theory, an inference which is consistent with the

conclusion arrived at in Chapter X. that there is no direct relation between the density of sea-water and the buoyancy of seeds and fruits, the floating capacities being as a rule far greater than the adaptation view would explain. Nature, it is held, has never made any provision for dispersal by currents, the buoyancy of seeds and fruits being, as concerns the currents, a purely accidental quality.

CHAPTER XIV

THE RELATION BETWEEN LITTORAL AND INLAND PLANTS

Professor Schimper's views.—Great antiquity of the mangrove-formation.—Problem mainly concerned with the derivation of inland from littoral plants.—Grouping of the genera possessing both coast and inland species.—Scævola. — Morinda. — Calophyllum. — Colubrina. — Tacca. — Vigna.—Premna.

In discussing the relation between the littoral and inland floras in the Pacific it will be at first necessary to pick up some of the threads of the various lines of investigation dealt with in the previous portion of this work. Apart from considerations connected with the genetic history of the plants concerned, when we come to inquire into the sources of any individual strand-flora, whether in the temperate or in the tropical regions, we arrive at the rough and ready inference that it is composed of "what the sea sends and the land lends." But it has been already shown that the relative proportion of the current-borne and in consequence widely dispersed plants in a strand-flora varies greatly in different regions. Thus in the Pacific islands, as typified by those of Fiji, about 90 per cent. have buoyant seeds or seed-vessels originally brought from distant localities; and in the tropics, as a rule, the average would probably be never under 75 per cent. On the other hand, in a temperate region the plants derived from inland would be most predominant, making up probably some three-fourths of the whole, whilst the proportion of current-dispersed plants hailing from distant places would be relatively few.

It is on this account that there is such uniformity in the general composition of the strand-flora over a large part of the tropics, since current-dispersed plants are widely spread. But in the temperate regions we find a great contrast in this respect.

There are, it is true, a few current-borne plants that one meets everywhere. For instance, Convolvulus soldanella is to be gathered on English beaches and on those of New Zealand and of the coast of Chile. But these littoral plants with buoyant fruits hardly give a feature to the strand-flora. A multitude of intruders, either characteristic of the inland flora of the region or confined only to the seaboard of that part of the world, also make their home on the beach and frequently endow a beach-flora with its leading features. The possible associations of plants on a beach in a temperate region are thus very great; and I have already discussed this in part in Chapter IV. as concerning the British shore-flora. One has only to look at a work like that of Dr. Willkomm on the vegetation of the strand and steppe-regions of the Iberian peninsula to realise how the few littoral plants familiar to the English eye cut but a sorry figure amongst the numbers of strange intruders from the arid regions inland. So again, as I found on the Chilian beaches, Convolvulus soldanella finds odd associates amongst the species of Nolana and Franseria that are peculiar to the coasts of that part of the globe (see Chapter XXXII.); and different grotesque American forms of the Cactaceæ with a Mesembryanthemum and a host of strange-looking plants descend from the arid slopes of the hills behind to keep company with the far-travelled English beach-plant (see Note 49). Or again, a glance at the pages of Professor Schimper's great work on *Plant-Geography* will bring the same fact home in a still more varied fashion.

Yet on tropical coasts the intruding inland element is also distinguishable, though it may influence only to a small degree the general character of the strand-flora. Dividing it, as we have described in Chapter V., into the plants of the sandy beach and of the mangrove-swamp, we find in the mangroves the most stable element and in the beach-plants those most liable to change. Professor Schimper observes that whilst the physiognomy of the beach-flora varies to some extent with the alterations in the inland flora, the mangrove-formation makes but a slow response to such changes. As he points out in his work on the Indo-Malayan Strand-Flora (p. 199), seeds and seedvessels are being continually brought down to the sea-coast through the agencies of rivers, winds, and birds; and in this manner, in the course of ages, the beach-flora is recruited from the inland plants. But for the mangroves such additions to their numbers are rarely possible. Whilst the same genera are often shared by both the beach

and inland floras, we have in the mangrove-formation families, sub-families, and genera almost peculiar to itself, and including plants, like those of the Rhizophoreæ, that in their characters betray but little kinship with others and give but little indication of their descent. The mangroves have remained through the ages as something apart from other coast-plants, isolated both in their history and in their characters, and especially distinguished by their "adaptations" to their surroundings.

Such is the line of argument followed by this eminent German botanist in his account of the development of a tropical strand-flora. In various parts of this work I have ventured to suggest that the mangroves may be the remnant of an ancient flora widely distributed over the lower levels and coastal regions of the globe in an age when vivipary (meaning, thereby, germination on the plant) was the rule rather than the exception. At such a period, as I imagine, the climatic conditions of the earth were much more uniform than they are at present, at least in the lower levels; and a warm atmosphere, charged with aqueous vapour and heavy with mist and cloud, enveloped a large portion of the globe. The mangroves, it may be remarked, are by no means universally distributed on tropical coasts in our own time. (Professor Schimper describes their distribution in his *Indo-malayische Strand-Flora*, pp. 85, 86, and in the English edition of his *Plant-Geography*, p. 409.) They are not found on rainless coasts even when under the Line, except where there happen to be large estuaries; but where a rank and luxuriant inland flora betokens a high degree of humidity, there they thrive. This is well illustrated on the rainless shores of tropical Peru, a locality described in Chapter XXXII. of this work.

Yet if, as it is here contended, the mangroves form a remnant of a once widely spread viviparous flora, it might be expected that the beach-plants of that age would have been also viviparous, and that with their present descendants, as well as with some of the inland plants allied to them, we ought to find in the anomalous structure of the seed some indication of the lost viviparous habit. This appears to be the case, as described in Note 50, with the Barringtoniæ, a tribe that has supplied some of the most characteristic beach-trees, and also with some genera of the Guttiferæ. Perhaps, indeed, when the seeds of several other littoral beach-trees come to be examined, for instance, Guettarda, analogous structures may be found.

Although the beach-flora of the tropics is less stable in its

composition than the mangrove-formation, it is not to be assumed that in the Pacific region or in the tropics generally it is at all modern in its character. Though in the main, no doubt, more recent than the mangroves, since it is likely that in early geological periods the swamp rather than the sandy beach formed the predominant feature of the sea-border throughout the tropics, yet it bears in several respects the impress of a high antiquity. There are few beach plants in the tropical Pacific that are not found over the tropics of a large portion of the globe, a circumstance that would in itself warrant our assigning a great age to the beach-flora; and it is highly probable that some at least of the beach plants of the Pacific that occur on the east and west coasts of tropical America are, for reasons given in Chapter XXXII., older than the barrier now interposed by Central America between the Atlantic and Pacific oceans. There are, it is true, a few species, like Acacia laurifolia and Drymispermum Burnettianum, which, on account of their restriction to the beaches of the Western Pacific and their lack of capacity for dispersal by currents, may be regarded as local productions; but for the great majority, ranging as they do over much of the tropics, it is not possible to determine when and where they assumed their littoral habits. That except in a few instances their home in some bygone age lay outside the Pacific can scarcely be doubted.

It is therefore to be expected that in a discussion of the relation between the strand and inland floras in the Pacific islands the problem will be mainly concerned with the possible derivation of inland from littoral plants. In such a discussion the relation between the beach and inland species of the same genus becomes a subject of great interest. It is a subject that had a peculiar fascination for Professor Schimper, who refers to it more than once in his pages; and though never able to take it up, he viewed it as a very promising field of inquiry. The question has been frequently alluded to in this work; and it is especially dealt with in one connection in Chapter II. It is there shown that whilst, as a general rule, the seeds or seedvessels of the coast species possess great floating power, those of the inland species of the same genus have little or none, and that both may have independent modes of dispersal, the first by currents, and the last through frugivorous birds.

A close connection between the beach and inland floras is apparently displayed in the circumstance that quite a third of the genera of the Pacific insular floras containing littoral species (some 70 in all, excluding the mangroves) possess in this region also

inland species. But the further examination of this interesting group of genera, which are enumerated in the list below, goes to show that the connection between the inland and coast species of a genus is by no means always so close, or of such a character, as one might have expected. It will not be possible, however, to do much more than indicate in this chapter the results of this inquiry; but the details will usually be found either in the separate discussion of the genus or in other parts of this work. For convenience of treatment these genera may be grouped in the following sections.

Grouping of the Plant-Genera of the Islands of the Tropical Pacific that possess both Littoral and Inland Species.

Section I. Where the littoral and inland species are most probably of independent origin, both possessing their own means of dispersal; Calophyllum, Hibiscus, Colubrina, Morinda, Scævola, Cordia, Ipomea, Vitex, Tacca, Casuarina.

Section II. Where the littoral species have probably given rise to inland species, and both still exist in the group of islands: Vigna, Premna.

Section III. Where inland species have been probably developed from littoral species no longer existing in the group: Canavalia, Erythrina, Sophora, Ochrosia.

Section IV. Where the littoral and inland species are evidently of independent origin, and there is no means of accounting for the existence of the inland species by agencies of dispersal at present in operation: Barringtonia, Pandanus.

Section V. Where in the same genus some inland species are derivatives of the coast species and others are of independent origin: Guettarda.

Section VI. Where the coast species, having little or no capacity for dispersal by currents, are regarded as derived from the inland species in one group of islands and as afterwards distributed to those in the vicinity: Eugenia, Drymispermum, Acacia.

Section I

This group, which includes those genera where the coast and inland species are regarded as of independent origin, both possessing their own means of dispersal, contains about half of the total

number of genera here concerned. We will first deal with the genera Calophyllum, Morinda, and Scævola, where the littoral species have buoyant fruits or seeds that are dispersed by currents, whilst the inland species have more or less non-buoyant fleshy fruits that could only be dispersed by frugivorous birds. Here the inland and coast species could have arrived independently at the island, and we are not called upon either on this ground or by reason of affinity of characters to connect the one with the other.

The genus Scævola is very typical of its kind and has been already in part discussed in Chapter II. The wide-ranging shore-species, S. Kœnigii, that is distributed over the Pacific may sometimes, as in Hawaii, be accompanied by numerous inland species, all endemic, seven of them being enumerated by Hillebrand ; or, as in Fiji and Tonga, there may be associated with it a solitary inland species, S. floribunda (see Note 51) ; or, as in Tahiti, it may exist by itself. On the other hand, as in the Kermadec Islands, a single inland peculiar species may alone represent the genus. The inland species have fleshy drupes which, as far as examined, have no floating power and possess no buoyant tissues in their coverings ; and their independent dispersal by birds cannot be doubted. The endemic character of most of the inland species of the Pacific islands is most probably due to the suspension of the transporting agency of frugivorous birds, just as the wide range of the solitary littoral species may be attributed to the uninterrupted agency of the currents. There is nothing in the description of the endemic species given in Hillebrand's *Hawaiian Flora* to indicate any especial genetic connection between the inland species and the beach plant, S. Kœnigii; and the occurrence of a solitary inland peculiar species in the Kermadec Islands clearly proves an origin independent of any littoral plant.

Morinda is another critical genus in this discussion. Besides the widespread littoral species (M. citrifolia) that is distributed by the currents and is also dispersed by man, there are in the Pacific islands a number of inland species, mostly climbers and denizens of the forests. In the *Index Kewensis* six are accredited to Fiji and five to New Caledonia. Hillebrand gives a peculiar Hawaiian species, and there is a widespread species (M. Forsteri) that ranges over the South Pacific from New Caledonia to the Marquesas and the Paumotu Islands. Since, as indicated in Chapter II. and in Note 8, the pyrenes of the fruits of the inland species are not dispersed by the currents and could readily be transported by frugivorous birds,

we are not called upon to connect them in their origin with M. citrifolia, the wide-ranging species of tropical beaches.

The fact of the dispersal of certain inland species of the genus over large areas of the tropics, such as in the case of Morinda umbellata through tropical Asia and Malaya, and M. Forsteri in the Pacific, is indeed sufficient proof that these inland plants are independent of any littoral species in the Pacific and possess their own means of distribution. Though the genus, comprising at least forty species, is mainly confined to the Old World, there are a few species in America; but M. citrifolia, the familiar beach species of the Old World and the Pacific, is not indigenous there, and, as far as I can gather, all the American species belong inland. Facts of distribution of this nature negative the possibility that the Pacific islands have received their inland species of Morinda through the intervention of the far-ranging littoral plant.

As respecting Calophyllum, which is represented all over the tropical South Pacific by the wide-ranging C. inophyllum and by a tree of the inland forests found also in Malaya and in Ceylon (C. spectabile), there are, apart from questions of affinity, grave objections against the derivation of the same inland species from the coast species all over this area. The fruits of the two inland species of Fiji, C. spectabile and C. burmanni, have sappy outer coverings and are quite suited for dispersal by fruit-pigeons. As observed in Chapter II. and Note 9, they have limited floating capacities and their dispersal by birds is necessary to explain their distribution. Since the timber is greatly valued by the Polynesians, it is not unlikely, however, that those islanders have assisted in the distribution of the inland species. It is not possible to do more than touch on this subject here; but it may be inferred that the history of Calophyllum in the Pacific has not been one that would warrant our regarding the inland trees as derivatives of a coast species.

There are other genera of this section where, for reasons of a different character, there is no cause for assuming that the inland species are derived from the coast species, or *vice versâ*. Thus, in Fiji, Casuarina equisetifolia, a widely distributed species of the Old World, occurs at the coast and in the scantily wooded plains behind; while C. nodiflora, a New Caledonian species, finds its home in the lower forests. There are many endemic species in Australia and New Caledonia; and we are not called on to connect together these two species in Fiji. In the same way we are not under any obligation in the case of the numerous inland species

of Ipomea of the Pacific islands to connect them with the coast species. They are all widely ranging species, and their seeds have been carried to the islands, each in its own fashion. So again with the inland species of Hibiscus found in the Polynesian islands and often cultivated, we cannot either from the point of view of dispersal or of affinity connect them with the far-ranging littoral species, H. tiliaceus, which belongs to a section of the genus distinct from those sections to which the inland species belong.

In a similar way there is no ground for supposing that Cordia aspera, an inland species confined to Fiji, Tonga, and Samoa, is derived from C. subcordata, the widely distributed littoral species of the Pacific and of the Old World, since they belong to different sections of the genus. But, apart from any question of affinity, the drupes of inland species of Cordia are known to be well suited for dispersal by frugivorous birds, though, unlike the littoral species above named, not adapted for transportal by the currents. The genus Vitex, which is represented by a wide-ranging littoral species in the Pacific (V. trifolia), appears to be associated with inland species only in Fiji, where one or two, seemingly endemic, occur. But there is nothing in Dr. Seemann's description of V. vitiensis, one of these species, that at all suggests its derivation from the strand species, a very variable plant that often extends far inland into the plains, adopting a different habit of growth in those localities. It is known that Vitex fruits can be dispersed both by birds and by currents. This genus is more fully discussed in a later chapter.

Of the genus Colubrina there seem to be only two Pacific species known—one the widely distributed shore-plant, C. asiatica, a straggling shrub with alternate leaves found in all the Pacific groups and on the beaches of much of the tropics of the Old World ; the other a tree, C. oppositifolia, with opposite leaves, that is peculiar to the Hawaiian islands, where it frequents the open-wooded and scrubby inland districts. The seeds of the shore-plant float unharmed for many months, whilst the fruits of the inland plant, which differ in some important respects (see Note 52), would float only for a week or two. The strand species is also quite at home inland in many parts of the world ; and there is nothing from the standpoint of affinity to indicate that in Hawaii it has given birth to an inland species so divergent in habit and in character. There is of course the difficulty of explaining how a plant like C. oppositifolia, with such a dry, unattractive fruit, could be indebted to birds for its original introduction into the group ; but the same difficulty arises with a host of Hawaiian plants. It

is, however, evident from its distribution over the islands of this archipelago that it possesses or has possessed some means of inter-island dispersal, and since it is not of much service to the aborigines we must look therefore to the bird.

In the instance of the genus Tacca there is in Fiji an inland species, T. maculata, associated with a wide-ranging beach species, T. pinnatifida, which also grows inland. The first-named is recorded from the north coast of Australia and from Samoa, and though, unlike the beach plant, its seeds are unfitted for dispersal by currents (see Chapter II.), they might be distributed by birds. Dr. Reinecke describes another inland species from Samoa, T. samoensis. The beach plant, T. pinnatifida, grows so typically (sometimes side by side with T. maculata) in the inland plains of Fiji that one would not be justified, apart from questions of affinity, in regarding it as the parent form of inland species in the Pacific islands.

For food and other purposes Tacca pinnatifida is or was much valued by the Pacific islanders, and it grows so abundantly that cultivation is rarely practised. That the Polynesians have aided the currents in the distribution of the plant there can be no doubt, and this is particularly indicated by its occurrence in Hawaii. The genus contains ten or a dozen species, of which at least three are peculiar to America; but T. pinnatifida, the characteristic shore-plant of the Old World, and according to Schimper the only one that can be so designated, is not found in America, where, as far as I can gather, there is no widely-spread beach species dispersed by the currents from which the peculiar species could have been derived. In the case of the Pacific species, however, it should be noted that I am not endeavouring to prove the improbability of the inland species having been derived from the coast species in other regions, as in Australia, but that my point is to show there is no reason to suppose that this has taken place in the Pacific. There is no difficulty in attributing the dispersal of inland species to birds; and we are therefore not called on to connect them with the beach plants.

SECTION II

This division includes those genera where the littoral species has apparently given rise to one or more inland species and both still exist in the same group of islands. Two genera alone, Vigna and Premna, come into this category. The first-named seems to present a good case for the derivation of an inland from a coast

species in Hawaii. Besides Vigna lutea, the beach species, which is found not only all over the Pacific islands but on the tropical beaches of the Old World, there are in Hawaii two endemic species (V. sandwicensis and V. oahuensis) that occur in the mountains, usually at elevations of from 1,500 to 5,000 feet; but I do not find any more inland species recorded from the other Polynesian archipelagoes. It may at first be noted that Vigna lutea, which in some parts of the world strays inland, displays considerable variety in its littoral station in the Pacific. Thus, in Hawaii, I found it sometimes on the sandy beach, sometimes on a rocky shore, and sometimes on the edge of old lava-cliffs overlooking the sea. In Fiji, though usually a trailer on the beach, it may become a climber hanging from the trees bordering the creeks in the mangrove-swamps. Though Hillebrand makes no mention of forms intermediate between coast and inland species in Hawaii, I found in one locality at the coast some specimens of Vigna lutea displaying the twisted pods and two callosities on the standard that are characteristic of V. sandwicensis, one of the inland species. The seeds of Vigna lutea float in sea-water unharmed for months, and they are to be found in the stranded drift of the Hawaiian and Fijian beaches, and floating in the drift of the Fijian rivers. I was unable to obtain the mature seeds of the inland species, and it has therefore yet to be determined whether they follow the rule in the loss of buoyancy. It may be added that a plant of Vigna lutea raised in Hawaii from seed displayed some small tubers of the size of a pea on its roots.

The case for Premna is stated in Note 32. In this genus, as with Vigna, the final test of experiment is needed; but the data at my disposal point to the probability that an inland species has here been derived from a littoral plant.

The summary of this chapter is given at the end of Chapter XVI.

CHAPTER XV

THE RELATION BETWEEN LITTORAL AND INLAND PLANTS (*continued*)

Inland species of a genus developed from littoral species originally brought by the currents but no longer existing in the group.—Illustrated by the Leguminous genera, Erythrina, Canavalia, Mezoneuron, and Sophora, and by the Apocynaceous genus, Ochrosia.—The Hawaiian difficulty.

SECTION III

HERE we have three genera of the Leguminosæ, namely, Erythrina, Canavalia, and Sophora, and one Apocynaceous genus, Ochrosia, in which it is considered that inland species have been probably developed from littoral species no longer found in the group. In this case the shore species, possessing buoyant seeds or fruits that are known to be dispersed by the currents, is absent from the particular group in which the inland species occurs ; and since the last-named displays no capacity for distribution by currents, or seemingly by birds, we are driven to infer that it was originally derived from a coast species, brought by the currents, that has since disappeared.

Hawaii is the only region concerned here; and these four genera may be said to well illustrate the particular "Hawaiian difficulty." If this explanation of the origin of the inland species is legitimate, then it offers us a mode of explaining still more perplexing cases in the Hawaiian flora, such as those relating to the endemic species of Mezoneuron (Leguminosæ) and to Hillebrand's Vallesia (Apocynaceæ), where there is apparently no littoral species known from any region.

Dealing with the three Leguminous genera, it is at first to be remarked that the great floating powers of the seeds of the littoral species are in all three cases to be attributed to the buoyant

kernel; whilst on account of the non-buoyancy of the kernel the seeds of all the inland species possess no floating power. Some very interesting points are raised in each of the three genera, and I will first deal with the genus Erythrina.

ERYTHRINA.

If we look over the Pacific islands in search of a critical locality for the investigation of the genetic relation between the littoral and coast species of Erythrina, we discover it, as far as I can gather, only in one group. In Fiji, Tonga, and Samoa we find only the littoral species; in Hawaii there is only an inland species; whilst in Tahiti occur both the littoral and the inland species—E. indica, the wide-ranging shore-tree of the South Pacific, and E. monosperma, the inland tree of Hawaii—the last found nowhere else in Polynesia, and confined to the Pacific. In Tahiti there are no other species, and it is between these two species that the connection, if it exists, is to be sought. (Further details relating to the genus are given in Note 53. In this place only the facts bearing on the argument will be discussed.)

The buoyant seeds of Erythrina indica are well known to be dispersed by the currents; whilst those of E. monosperma, as obtained from Hawaii, have no floating power and sink at once, or in a day or so, even after drying for two years. In Tahiti the first-named species is a characteristic plant of the beach, whilst the last grows there in the valleys and on the mountains up to elevations of 700 to 800 metres. We have now to inquire whether there is any decided affinity between the two species, and whether the divergent characters of the inland species can be connected with its station. With regard to the first query we may quote in reply the observation of Drake del Castillo, that as concerning the foliage and the inflorescence E. monosperma is very nearly related to E. indica, differing only from it in the more hairy calyx, in the more permanently tomentose and much shorter pod, and in the paucity of seeds (one or two in number).

We will now see whether it is possible to connect these differences in character with differences of station. Neither Nadeaud nor Drake del Castillo give precise descriptions of the station of Erythrina monosperma in Tahiti; but Nadeaud and Lepine remark that it grows on precipices as well as in the valleys on the north or dry side of the island; and we may infer that it

affects exposed dry rocky stations. In Hawaii, according to Hillebrand, it is found on the dry rocky hills and plains of all the islands up to 1,000 feet. I was particularly interested in this tree whilst in the group, and found it in the large islands of Maui and Hawaii thriving in rocky arid districts of little rainfall, accompanied by Cactus opuntia, Ricinus communis, and Cæsalpinia bonducella. It is often to be observed on scantily vegetated lava-flows, a solitary tree growing here and there out of a crack in the old lava, or it may dot the rocky slopes of some barren declivity. I found it in the dry gulches behind Lahaina at elevations of 800 to 1,200 feet above the sea, growing amongst huge blocks of stone in clumps of ten or twelve trees. When one contrasts the inland station of E. monosperma with that of E. indica on the beach where the atmosphere is more humid and the conditions more suited for plant-growth, it appears probable that the differences between these two species may be largely connected with station, especially as regards hairiness and the diminished size of the pods.

Assuming, therefore, that Erythrina monosperma is but the inland form of E. indica and that the differences between the two species are mainly an affair of station, we have next to account for the occurrence of the inland species in Hawaii without the littoral species. The agency of currents in explanation of the existence of E. monosperma in Hawaii is at once excluded, since the pods dehisce on the tree, and the seeds, as already remarked, have no floating power. Nor does it seem likely that beans half an inch (13 mm.) long could be transported unharmed in a bird's stomach over the two thousand miles of sea that intervene between Tahiti and Hawaii. Yet one cannot doubt that the pyrenes and "stones" of genera like Coprosma, Nertera, Cyathodes, and Osteomeles have been carried by frugivorous birds to Hawaii. But a bean is somewhat different from the crustaceous pyrene of Coprosma or the hard "stone" of Cyathodes; and although, as indicated by the occurrence of an endemic species of Erythrina in Fernando Noronha, birds may carry large beans unharmed over a couple of hundred miles of sea, one hesitates to conclude that they could effect this when the tract of ocean to be traversed is ten times as great. There are again reasons for believing that the seeds of Erythrina monosperma are particularly ill-suited for dispersal by birds, since, notwithstanding their hardness, they soon absorb water through the micropylar opening; and they germinated so readily in my experiments that the digestive juices in a bird's stomach would probably soon find access and destroy the

kernel. It is, however, known from the observations of the Messrs. Layard in New Caledonia that a small crow and different species of parrots feed on the seeds of Erythrina, and they may aid in the local dispersal (*Ibis*, vol. 6, 1882).

To admit man's agency in carrying to Hawaii the seeds of a tree which is only useful in supplying him with light wood for his outriggers and his fishing-net floats would compel us to place in the same category a great number of plants in some way useful to him which are recognised as indigenous. The Polynesian ransacks the vegetable world for his wants, and carries with him in his migrations only his food-plants and the seeds of his sacred trees.

There remains then the possibility that the parent species, Erythrina indica, was once in Hawaii but has since disappeared. In order to establish this, it will be requisite to show not only that the extinction of a shore-plant is probable, but also to explain why the new species has selected such arid inland localities for its stations, to account for the loss of buoyancy of the seeds, and, if possible, to give an instance of the production of a new species of Erythrina in a small isolated oceanic island.

A study of the special circumstances of Hawaii leads one to conclude that a shore-tree may become extinct in one of two ways. It may be exterminated by insect pests, or it may be forced inland through unsuitable coast-conditions and there be lost in the resulting new species. One characteristic shore-tree, Cordia subcordata, has indeed been almost exterminated by insects, and even Erythrina monosperma is now from the same cause on its road to extinction (see Note 53); but there is no indication of their leaving modified descendants behind that are pest-proof. The most probable view then is that the littoral tree, having been driven inland through the unsuitability of the coast-conditions, such as lack of beaches or want of moisture, has there become modified. This is what has really happened, as I have shown, with Cæsalpinia bonducella in Hawaii. As indicated in Chapter XVII., this characteristic beach-plant has here been driven off the beach. There would thus be no difficulty in assigning a reason why a littoral tree like Erythrina indica should select arid localities when it extends inland, since, as is pointed out in Chapter IV. and in other parts of this work, the plants of the beach and of the arid inland district possess the same xerophilous habit.

With regard to the loss of buoyancy of the seeds in the case of

Erythrina monosperma, it may be remarked that this is precisely what has happened with the seeds of Cæsalpinia bonducella, its usual associate on the old lava-wastes in Hawaii, and with an inland species of Cæsalpinia in Fiji. It is argued that the same thing has occurred with the inland Hawaiian species of Canavalia and Sophora, as shown in later pages of this chapter. It has certainly happened with the inland form of Afzelia bijuga in Fiji, a tree dealt with in Chapter XVII. These are all Leguminous genera; and in all of them, with the exception of Cæsalpinia, where the floating power arises from a central cavity in the seed, the seeds of the littoral species possess, like Erythrina indica, buoyant kernels. Whilst most littoral plants with buoyant seeds or fruits retain the floating capacity of the seed or fruit when they extend inland, the Leguminosæ often offer exceptions to the rule.

That inland endemic species of Erythrina can be developed in isolated islands is illustrated by the existence in Fernando Noronha, some two hundred miles from the coast of Brazil, of a peculiar species, E. aurantiaca, described by Mr. Ridley. Here also is found an inland species of Guettarda peculiar to the locality; but in neither genus does the littoral species occur.

Many difficulties will yet have to be explained before it can be finally established that Erythrina monosperma has been derived from E. indica or some similar shore species that was originally dispersed by the currents; but we are almost driven towards such a view, since it is hard to believe that the beans were carried to Hawaii by birds over some two thousand miles of sea. Observers in other regions where littoral and inland species of the genus occur may perhaps devote their attention to the relation between the two; and if they are able to supplement observation and experiment by a microscopical investigation, some interesting results would be obtained. For instance, I would suggest that in Queensland a thorough examination of the littoral E. indica and the inland E. vespertilio might be undertaken; or perhaps there may be some other littoral form.

With the two other Leguminous genera, Canavalia and Sophora, to be immediately discussed, we have for the most part the same questions raised. Both possess wide-ranging current-dispersed littoral species in other parts of the Pacific, but only endemic inland species with non-buoyant seeds in Hawaii. The pivot of the discussion will be here also the impracticability of these inland species ever having reached the Hawaiian Islands

through the agency of the currents, and the great difficulty in believing that their beans were carried unharmed by birds over half the breadth of the Pacific Ocean. If we reject alike the current, the bird, and the parentage of a lost littoral species, we must fall back on the continental hypothesis, against which in the case of Hawaii the evidence is overwhelming.

Canavalia.

This genus is represented in the tropical islands of the South Pacific from Fiji to Tahiti by three littoral species, none of which have been found in Hawaii, where only an endemic inland species exists. Reference will alone be made here to such facts as bear on the probable history of the mysterious Hawaiian species, additional particulars being given in Note 54. The littoral species, Canavalia obtusifolia (D. C.), C. sericea (Gray), and C. ensiformis (D. C.), have buoyant seeds and are dispersed by the currents; whilst the inland Hawaiian species, C. galeata (Gaud.), a forest climber peculiar to that group, has non-buoyant seeds. We thus have repeated the problem of Erythrina monosperma. The absence of the littoral species from Hawaii can scarcely be attributed to the failure of the currents, since Ipomea pes capræ, which accompanies C. obtusifolia as a beach-creeper all round the tropical globe, is present on the Hawaiian beaches. Nor can it arise from lack of floating-power on the part of the seeds, since experiment indicates that the seeds of C. obtusifolia will float for months unharmed in sea-water. Nor can it be ascribed to climatic conditions, since this tropical shore species extends into cooler latitudes than those of the Hawaiian Islands, being found in the Kermadec Group and in the Bermudas, which are subtropical both in position and as regards much of their vegetation. The reason perhaps we may never learn from the plants themselves, though it may be possible to obtain some light on the problem from outside sources.

Canavalia galeata differs much in its habits, as well as in some of its characters, from the existing littoral species of regions outside the Hawaiian Group. It is a stout climber ascending the forest trees to a considerable height, though, as is indicated in Note 54, the shore species sometimes display a tendency in the same direction. It is described by Hillebrand as occurring "on all islands, in forests up to 2,000 feet." Like those of the inland species of Erythrina (E. monosperma), its seeds sink in sea-water even after being kept for four years, nor could the pods be utilised

for dispersal by the currents, since they float, when unopened, only for four or five days. Here also, as with Erythrina, the seeds of the inland species no longer possess the buoyant kernels to which the floating capacity of the seeds of the coast species is due. Though we have to exclude the currents, we can scarcely in its case appeal to bird-agency when we wish to account for the transportal of the original seeds to Hawaii, as that would imply that birds can carry beans nearly an inch, or 2 to 2·5 centimetres, in length unharmed in their stomachs over a tract of ocean some 1,500 or 2,000 miles across. We should have to learn much that is unexpected of the modes of dispersal of the Leguminosæ before we could accept such an hypothesis.

Canavalia galeata indeed presents to the student of dispersal one of the enigmas of the Hawaiian flora; and it should be noted that the mystery of its distribution is concerned not only with the means of transportal of the seeds of the original species to the group, but also with its present dispersal among the islands. It is, however, suggestive that Dr. Hillebrand mentions two varieties, one of them found on Kauai, with somewhat smaller seeds; so that some inter-island differentiation is evidently in progress. No attempt is made here to connect this inland species directly with the absent beach-plants. That is a matter for the systematist; but we are not tied down to existing shore-plants in finding an ancestor, since the common parent of the littoral and inland species may have been a shore-plant dispersed by the currents.

Mezoneuron.

Another closely parallel instance, offering, from the standpoint of dispersal, the same difficulties presented by Canavalia galeata, is to be found in Mezoneuron kauaiensis (Hillebr.), a tall inland shrub also peculiar to the group and belonging alike to the Leguminosæ. The difficulties are so nearly identical that the same explanation will have to cover both; but it is significant that with Mezoneuron there is no littoral species to which we can appeal to extricate us from the difficulty. Yet the genus is related to Cæsalpinia, and the species was first described by Mann as C. kauaiensis, so that it may have once possessed a littoral species that has ceased to exist as such. When we come to discuss Cæsalpinia and Afzelia (Chapter XVII.) we shall obtain from those genera many suggestions as to the probable past of Canavalia

galeata and Mezoneuron kauaiensis, two of the greatest riddles presented by the Leguminosæ of Hawaii.

The flat seeds of this species of Mezoneuron measure about an inch (2·5 cm.), and seem most unsuitable for dispersal by birds over a wide extent of ocean. Nor can we appeal to the currents, since my experiments in Hawaii show that the seeds have no buoyancy and that the pods only float for a week in sea-water. Dr. Hillebrand records this shrub from Kauai, Oahu, and Maui ; I found it also on the lower slopes of Hualalai in Hawaii and therefore the same question of inter-island dispersal here presents itself that was connected with Canavalia galeata, since we have also to explain the transport of the seeds between islands 70 to 150 miles apart. The critical point in the history of these two enigmatic inland plants of the Hawaiian Islands was doubtless concerned with the loss of buoyancy of the seeds of the original littoral plant. It will subsequently be shown that this is what is now in actual operation with Cæsalpinia and Afzelia in different parts of the Pacific.

SOPHORA.

In this genus, as in Erythrina and Canavalia, we have a littoral species, Sophora tomentosa, that ranges over the tropical beaches of the globe, including most of the islands of the Pacific, but does not occur in Hawaii, where the genus is represented by an endemic inland species, S. chrysophylla. Here also we find the shore-species with seeds capable of floating for months on account of their buoyant kernels, and the inland species with seeds that sink even after years of drying (see Note 56). Unless other inland species of Sophora have recently been described from the tropical Pacific, the Hawaiian species is the only one of its kind known from this region.

But the problem wears a different aspect in the case of this genus, since the endemic inland species of Hawaii is a tree of the mountains where a temperate climate prevails, whilst Sophora tomentosa is a shrub of the tropical beach that only at times extends into subtropical latitudes. The Mamani tree, as the Hawaiians name S. chrysophylla, extends up to 9,000 or 10,000 feet above the sea, forming, with Myoporum sandwicense and one or two other trees and shrubs, the highest belt of the forest in the larger islands. It is in the open woodland between 6,000 and 7,000 feet that it is most at home, and here it attains a height of 20 to 30 feet. It descends in places to as low as 2,000 feet above

sea-level ; but here is living under uncongenial conditions, and, like Myoporum sandwicense, becomes dwarfed and shrubby. The climatic conditions under which S. chrysophylla thrives in the Hawaiian mountains are therefore those of the temperate zone. From the data given in Chapter XIX., the mean annual temperature at an elevation of 6,000 to 7,000 feet would probably be about 55°, the average temperature of New Zealand.

We must therefore look to the temperate and not to the tropical zone for the home of the parent species of Sophora chrysophylla ; and if it was originally derived from a shore-plant dispersed by the currents, the widespread S. tomentosa could scarcely have been the species concerned. But this strand-plant is disqualified for another potent reason, since it belongs to a different section of the genus. Whilst S. tomentosa belongs to the section possessing smooth pods, S. chrysophylla is referred to the section Edwardsia having four-winged pods, which comprises about ten species found in Chile and Peru, Hawaii, New Zealand, Further India, and the Isle of Bourbon. What strange principle in distribution, we may fitly ask, has linked together in this odd fashion the continents of the Old and New World and the islands of the Indian and Pacific oceans ?

Yet, discredited as Sophora tomentosa is as a possible parent of the Hawaiian mountain species, it may yet afford us a clue. It is significant that the distribution of this wide-ranging beach-shrub in the tropics of the southern hemisphere is almost coterminous with that of Sophora tetraptera, a species widely spread in the south temperate zone from Chile to New Zealand and extending towards the tropics as far as Juan Fernandez in lat. 33° S. and to Easter Island in lat. 27° S. Though not strictly a beach-plant, S. tetraptera is a plant of the sea-border ; and it is remarkable, but not surprising, how in New Zealand, one of its principal homes, its behaviour in respect of its vertical distribution presents a great contrast to that of S. chrysophylla in the tropical latitudes of Hawaii. We have seen that, in Hawaii, S. chrysophylla, which thrives as a tree 20 to 30 feet high in the mountains, becomes shrubby when it descends to the lower levels. In New Zealand, S. tetraptera is, as we learn from Kirk, a prostrate shrub in the mountains, whilst in the lower elevations towards the sea it becomes a tree 30 and even 50 feet in height. It can scarcely be doubted that, if we exchanged the habitats of these Hawaiian and New Zealand species, each would to a great extent take up the other's station and the other's habit.

The whole problem of the dispersal of Sophora was brought immediately to my notice at Corral, in latitude 40° S. on the coast of Chile. Here a small tree of the section Edwardsia was growing in fruit on the lower slopes of the hills, becoming bushy when descending to the beach. Specimens of its four-winged pods have been identified at the Kew Museum as those of Sophora tetraptera; and, as far as the pod is concerned, I cannot distinguish between my specimens of the Hawaiian S. chrysophylla and the Chilian species. Subsequently I found the buoyant seeds of the same plant amongst the stranded beach-drift at Bahia San Vincente, nearly 200 miles further north. This led to my experimenting on the capacity of the plant for dispersal by the currents, and as a result it was ascertained (see Note 56) that whilst, as in the case of S. chrysophylla, the pods floated only one or two weeks, the seeds on account of their buoyant kernels floated for several months in sea-water, retaining their power of germination. The Chilian plant thus differs significantly in its capacity for dispersal by currents from the Hawaiian species, the seeds of which sink in sea-water even after years of drying.

The Mamani tree in Hawaii had always been an object of great interest to me. I was attracted by the mystery surrounding its origin and had long suspected that the clue was to be found in the non-buoyancy of its seeds and in the absence of a littoral species of the genus. When in Fiji it was to the littoral Sophora tomentosa that I looked in vain for a solution of the riddle, and seven years afterwards on the coast of Chile a solution of this enigma of the Hawaiian mountains presented itself in the form of an argument somewhat in this shape.

On account of the elevated station of the Mamani tree (S. chrysophylla) in Hawaii it is to be inferred that the original species was a plant of the temperate regions or of the uplands of some tropical mountains. If it has had its origin in some shore-plant dispersed by the currents, that species can only now be found on the coasts of extra-tropical regions. Such a maritime plant had buoyant seeds; and plants of this type are presented by Sophora tetraptera and its allied species that are at home in the cool latitudes of the southern hemisphere, as in Chile and New Zealand. No difficulty, as I argued, could be connected with the loss of buoyancy of the seeds of the Hawaiian mountain species, since it follows the general principle (laid down in Chapter II.) that in the same genus coast species have buoyant seeds or fruits, and inland species those that sink; and in support of this view it was

recalled that this is what happens to the seeds of Cæsalpinia bonducella and Afzelia bijuga when the plants extend inland in the Pacific islands. It was held, in short, that the original form of Sophora chrysophylla in Hawaii was a coast plant with buoyant seeds, and therefore indebted for its presence to the currents. Hailing from an extra-tropical region, it abandoned the beach and found suitable conditions of existence in the mountains, where it underwent specific differentiation. Such was the explanation that presented itself to me on a Chilian beach.

The first objection that offers itself against this view is that Sophora chrysophylla is one of several species characterising the antarctic element of the mountain flora of Hawaii, and that many of these plants, such as those of the genera Astelia, Coprosma, Gunnera, Myoporum, &c., could only have reached these islands through the agency of frugivorous birds (see Chapter XXIII.). There is, therefore, something to be said for this mode of dispersal; but though one can understand how hard seeds and the "stones" and crustaceous pyrenes of fleshy fruits might be transported unharmed in a bird's stomach half-way across the Pacific Ocean to the distant group of Hawaii, it is difficult to understand how Leguminous seeds, except in such cases as Tephrosia piscatoria, could be ejected unharmed by a bird after an ocean passage of some 1,500 or 2,000 miles. Yet evidence pointing to such a possibility is not lacking. It was pointed out by W. O. Focke (*Nat. schaft. Ver. zur Bremen*, Abhandl., Band 5, 1876) that for many Leguminosæ we are driven to the agency of birds in order to explain their dispersal. In this connection he mentions the case of a pigeon killed by some beast of prey that he found in his garden in the early winter. In the following spring he noticed numerous seedlings of Vicia faba sprouting up from amongst the feathers that alone remained of the bird. In this observation he detected the normal method of the dispersal of the Leguminosæ by birds, the seeds not being ejected by the bird but being set free by its death. It is well known that Darwin had this idea in his mind when he conducted his experiments on the dispersal of seeds; and reference may here be made to one that is recorded in *More Letters of Charles Darwin* (i., 436). Out of a number of seeds left in the stomach of an eagle for eighteen hours, the majority were killed; but amongst the few that germinated afterwards was a seed of clover (Trifolium). If such a bird had carried a Sophora seed to Hawaii, this would have involved a continuous flight of, on the average, 100 miles per hour for a period of fifteen to twenty hours.

This would just come within the limitations laid down by Gätke as regards length and velocity of flight—a subject discussed in Chapter XXXIII.

We will now turn to the Sophora seeds themselves for evidence of their capacity of surviving the perils of such a journey. The seeds of Sophora chrysophylla, which are about a quarter of an inch (6 to 7 mm.) in length, possess unusually hard coverings for the order, and in that respect appear fitted for dispersal by animals. Indeed, in the large island of Hawaii wild pigs and sheep feed on the pods, and no doubt aid in the distribution of the plant over the island through the germination of ejected undigested seeds. But since the species is found on most of the larger islands, it is apparent that to birds we must look for the explanation of its inter-island dispersal. Mr. Wilson, in his *Aves Hawaienses*, remarks that one of the Hawaiian finches (Loxioides) feeds on the seeds of this tree, which probably, he adds, also serve as the food of Chloridops kona, another big finch; and it is to be inferred from the observations of Mr. Perkins, quoted by Mr. Evans in his book on Birds, that the Drepanididæ, a family peculiar to Hawaii, are in the habit of splitting the pods of trees like Acacia koa and Sophora chrysophylla to obtain the seeds. It would, however, seem that the agency of birds confined to these islands does not carry us very far when we wish to explain the original transport of the seeds over a breadth of ocean of some 1,500 miles and more. Yet we know that this must have happened with some of the Hawaiian plants, such as Osteomeles anthyllidifolia and Nertera depressa, that are not confined to these islands and possess fruits that would attract frugivorous birds. But whether it has occurred with the dry beans of the Hawaiian species of Sophora is another matter.

On the whole I am inclined to the view, bearing in mind the general indications of the Leguminosæ in the Pacific, that S. chrysophylla originally reached Hawaii as a littoral plant through the agency of the currents. Many points still need investigation; but it may be pointed out that South America probably received Sophora tetraptera from New Zealand by the West Wind Drift Current.

OCHROSIA (Apocyneæ).

This genus seems to offer the strongest testimony in support of the derivation of an inland species from a strand-plant. The drupes are so large, the minimum size of the "stone" being 1½ or

2 inches (37 to 50 mm.), and so dry and unattractive for birds, that any other agency but that of the currents appears to be out of the question. Indeed their dry appearance would suggest to my readers that only birds of the habits of the ostrich would venture on such a diet. It is, however, worth noting that whilst in the Keeling Islands I learned that a cassowary that had been kept on the atoll was a very efficient distributor of the seeds of Ochrosia parviflora, scattering the undigested stones everywhere, and causing the young trees to become so numerous that they had to be destroyed. A similar habit of the cassowary in the Aru Islands is recorded by Beccari, where the dry fruits of a palm, 2½ inches across, are swallowed by these birds and the seeds dispersed. Cassowaries are active agents in dissemination, for they swallow every kind of pulpy fruit, and convey them long distances undigested; they are also excellent swimmers and traverse considerable expanses of water (Beccari, quoted in *Chall. Bot.*, iv., 297, 313).

Modern ornithologists would probably not object to our appealing to the former volant habits of the cassowary and its allies even across a wide tract of sea; but, excepting in New Zealand and its vicinity, such birds are not at our disposal in the island groups of the open Pacific. There is a possibility that the extinct Columbæ and other exterminated birds of the Mascarene Islands might account for some anomalies in their floras; and in Chapter XVI. reference is made to the fact that these islands possess more endemic species of Pandanus than any other oceanic groups, a genus possessing drupes that in the case of inland species seem unfit for any mode of dispersal with which we are familiar. In the islands of the tropical Pacific, however, it is not possible to find such a way out of the difficulty, since, as shown in Chapter XXXIII., the birds are lacking.

The genus, according to the *Index Kewensis*, includes about ten species distributed over the islands of the Indian Ocean, and found also in Malaya, Australia, and throughout the Pacific. It is essentially an insular genus, and two at least of the species are wide-ranging littoral trees, one, Ochrosia borbonica, mainly distributed over the islands of the Indian Ocean and of Malaya, and the other, O. parviflora, chiefly of the islands of the Pacific. It will be out of place to deal here in any detail with this interesting genus, and my remarks will be confined to such matters as concern the origin of the inland species of the Hawaiian Islands, species that are peculiar to that group. Some confusion has pre-

vailed amongst different authors in the determination of the limits of the various species, and to avoid this I have mainly followed Schumann in his monograph on the order (Engler's *Naturl. Pflanz. Fam.*, Theil 4, Abth. 2, 1895), as indicated in Note 57.

Besides the littoral species Ochrosia parviflora, Hensl., that ranges over most of the archipelagoes of the Pacific from the Solomon Islands to Tahiti, but is not found in Hawaii, we have in the Pacific, O. elliptica, Lab., of New Caledonia and Fiji; another species of New Guinea and the Ladrones; and one or two inland species of Hawaii. Ochrosia parviflora was familiar to me on Keeling Atoll, in the coral islets of the Solomon Group, and on the islets and coasts of certain parts of Fiji. Its fruits, which are dispersed by the currents, were found amongst the stranded drift of the Keeling and Fijian beaches. Although usually a coast-tree in Fiji, it came under my notice in one locality growing inland; and it is a very suggestive circumstance in connection with the inland species of Hawaii, that in Tahiti this tree is only described by the French botanists as growing in the mountains at elevations of 700 to 800 metres above the sea, it having for some reason abandoned the beach. The process which we thus see in operation in Tahiti is completed in Hawaii, and we there find a peculiar inland species far away in the interior of the islands which is placed by Schumann in the same section of the genus with the littoral O. parviflora, that is not, however, found in the group. It may be remarked that Gray describes only one species from Hawaii, O. sandwicensis, but Schumann makes two species of it—one, O. compta, Sch., peculiar to the group and referred to the same section as O. parviflora; the other, the original species of Gray, which he considers as probably a variety of O. borbonica. These determinations of the German botanist, who had no theory to serve, are especially interesting. It is with the littoral trees now missing from the Hawaiian beaches that he compares the inland species of the group, trees now chiefly characteristic the one of the Indian Ocean and the other of the South Pacific; and we can scarcely doubt that originally one littoral tree ranged over both oceans.

Hillebrand describes Ochrosia sandwicensis of Gray as a shrub or small tree, 6 to 12 feet in height, growing in the open woods of the lower and middle regions on all the islands. Its dry ellipsoid fruit is two inches (5 cm.) long, and possesses a thin suberose covering on one side and a very thick woody endocarp, one-quarter to one-third of an inch (6 to 8 mm.) in depth. The other species which he

characterises as a variety is not so generally distributed in the group. We have to explain not only how the original species reached the group, but also how they have been distributed over the islands. The currents could scarcely have transported the fruits as we now see them. Those of O. sandwicensis have only a trace of a buoyant covering, and, judging from some fruits that I examined, they could possess little or no floating power. Even the most enthusiastic advocate of dispersal by birds must pause here; and there remains the view, supported by evidence of a striking character, that the inland Hawaiian species are derived from littoral species that, having been originally brought by the currents, like O. parviflora in Fiji, abandoned the beach and took to the mountains, where they have become differentiated.

It is probable that the lesson of Ochrosia in Hawaii can be applied to one or two of the other Hawaiian "difficulties," and that plants that now set at defiance all the attempts of the student of dispersal to explain their occurrence in this group may have commenced their existence in these islands as littoral species brought originally by the currents and afterwards driven off the beach. One of the greatest enigmas of the Hawaiian flora is connected with another small Apocynaceous tree peculiar to the group and described by Hillebrand as Vallesia macrocarpa and by other Hawaiian botanists as a species of Ochrosia. Schumann, however, places it in a new genus, Pteralyxia, near to Alyxia, a genus already in the islands. However this may be, its dry drupaceous fruits two inches (5 cm.) in length, and its pyrenes almost as long, could never have been transported as such by the birds of our own time; and if they could have been carried in the stomach of a bird given to the dietetic humours of the cassowary, such birds in their trans-oceanic passages would have left some trace behind in the groups of the mid-Pacific. In our perplexity we read again the lesson of Ochrosia.

Summary of Chapter (see end of Chapter XVI.).

CHAPTER XVI

THE RELATION BETWEEN LITTORAL AND INLAND PLANTS (*continued*)

The Fijian difficulty.—Inland species of a genus possessing fruits not known to have any means of dispersal through agencies now at work in the Pacific.—Pandanus.—Its remarkable distribution in oceanic groups.—To be attributed perhaps to extinct Columbæ or extinct Struthious birds.—Barringtonia.—Guettarda.—Eugenia.—Drymispermum.—Acacia laurifolia.—Conclusions to be drawn from the discussion.—Summary of chapters XIV, XV, XVI.

SECTION IV

HERE we deal with two genera, Pandanus and Barringtonia, where inland endemic species occur in the same group with the wide-ranging coast species, but possess fruits concerning which it is either difficult or almost impossible to suggest a mode of dispersal by existing agencies. This section is especially concerned with Fiji, and represents the peculiar "Fijian difficulty" that is illustrated by other genera as—for instance, the Coniferous genus Dammara—which are not in any sense littoral. Further investigation is, however, requisite in the case of Barringtonia, and to a less degree with Pandanus; and I can only here point to the general indications of the data at my disposal. We have in these genera to assume either that the inland species are derived from the coast species, or that the seeds were brought by one of the extinct birds of the Western Pacific, by a megapode or by one of the Columbæ, or by some Struthious bird like the moa or the cassowary, or, if these two assumptions fail, that there has been a continental connection through the islands to the westward with the mainland beyond.

PANDANUS.

I take this genus first because the recent monograph on the Pandanaceæ by Dr. Warburg (Engler's *Das Pflanzenreich*, 1900)

enables me to tread on relatively safe ground in making my deductions. The three genera of the order, Freycinetia, Pandanus, and Sararanga, each tell their own story; and in each and all of them I have taken an especial interest from the standpoint of their dispersal. Freycinetia is fully discussed in Chapter XXV., and presents no difficulties respecting its dispersal. In the discovery of Sararanga the author has had a share. It was first established by Mr. Hemsley from specimens sent by me to Kew in 1885; and it has received from the botanist the name given to it by the natives of the islands of Bougainville Straits in the Solomon Group, where I first collected it. It contains only one species and was also discovered by Dr. Beccari, the celebrated Italian botanist, in Jobie Island, New Guinea. From the other two genera of the order, Pandanus and Freycinetia, it stands quite apart; and it apparently presents us with a relic of some ancient flora on the western borders of the Pacific. Its fleshy drupes (one-half to three-quarters of an inch in size) inclosing several small osseous pyrenes seem suited for dispersal by birds; and it is not at first sight easy to understand why its distribution should be so limited, unless this is connected with its diœcious habit (see Guppy's *Solomon Islands*, p. 302; *Journ. Linn. Soc. Bot.* vol. xxx.; and Warburg's monograph).

It is, however, with the genus Pandanus that we are here especially concerned. If the advocate of the previous continental connections of Fiji and the groups around were to look for evidence in support of his views, he apparently could not do better than take this genus. Whilst P. odoratissimus, the littoral species of tropical Asia and Malaya, is found on the coasts of almost all the Pacific islands from Fiji to Tahiti and northward to Hawaii, it is only in the archipelagoes of the Western Pacific, namely, in Fiji and Samoa, that inland endemic species have been found. (Such species occur also in the more western islands not dealt with here—New Caledonia, Solomon Islands, &c.) Not even in Hawaii, with all its botanical evidence of antiquity, has an inland endemic species been found, although the coast species extends miles inland, and for nearly 2,000 feet up the mountain slopes. When, however, we turn to Fiji and Samoa, we find in each group two endemic inland species. To endeavour to connect the inland species of Fiji and Samoa with the widespread littoral Pandanus odoratissimus, that owes its dispersal largely to the currents, is out of the question, at least for the student of plant-dispersal, since they belong to different sections of the genus, and in their characters are often far removed (see Note 58).

As regards the agency of birds, it is of course possible that fruit-pigeons that can disperse the "stones" of Canarium and Elæocarpus could transport the smaller drupes of Pandanus to oceanic islands like the Fijis, Samoa, and the Mascarene Islands; and in Note 58 reference is made to the size of the drupes of the endemic species of Pandanus in those groups. But my difficulty is that I have not come upon any record of birds eating these fruits; and I should imagine that amongst living birds only those like the cassowary and its kin would prefer such a kind of diet; whilst the only pigeon that could have ever attempted it must have been able to swallow pebbles like the dodo. It is remarkable that the Mascarene Islands, the home of the extinct Columbæ, possess more endemic species of Pandanus than any other groups.

Dr. Warburg points out that, with the exception of some three or four species dispersed by the currents (P. dubius, P. leram, P. polycephalus, P. odoratissimus), almost all the species (156 in number) are very restricted in their areas. When we look at his table of the distribution of the genus we notice that, excepting the islands of the Hawaiian and Tahitian regions, nearly all the elevated or mountainous islands of the tropical and subtropical latitudes of the Indian and Pacific oceans have their peculiar species, whether in the case of Mauritius, Rodriguez, Réunion, and the Seychelles in the one ocean, or of Lord Howe Island, New Caledonia, Fiji, and Samoa in the other. The student here hesitates even to raise the question of present plant-dispersal in the face of such evidence of isolation all over the area of the genus. He is almost inclined to evade the issue and to place the matter beside that of the dying or extinct Columbæ that have been found in some of these islands, as in Mauritius, Rodriguez, Réunion, and Samoa.

For reasons above given in the instance of Fiji and Samoa, it would seem futile to attempt to connect in their origin the inland with the coast species; and it may be inferred that, excepting the few dispersed by the currents, the species are in the main inland in their stations. Those peculiar to Fiji, for instance, occur in the swampy forests of the lower regions of the interior, as well as high up towards the mountain summits. When traversing the Fijian forests I often used to speculate on the modes of dispersal of the plants familiar to me; but the sight of a strange Pandanus usually brought my speculations to a close. Many of the enigmas of insular floras would be solved if we could interpret aright the 156 species of Pandanus that are enumerated and described by

Dr. Warburg in his monograph. Observers like myself obtain little peeps into the conditions of existence of these interesting plants; and the travelled botanist, who becomes a systematist in his later years, attains to a far more extensive view, yet even he can only penetrate the mystery for a little way.

It is doubtful whether Pandanus odoratissimus, the shore-tree of the tropical beaches of the islands of the Pacific and Indian oceans, of Australia, Malaya, and Southern Asia, can aid us much in any one locality, since its distribution has no doubt been often assisted by man. Yet it is probable that the currents have played a predominant part in its dispersal. Its fruits occur commonly in beach-drift, both in the Indian and Pacific oceans, and are often incrusted with serpulæ, polyzoa, and cirripedes. At certain seasons the currents bring them to Keeling Atoll in abundance. When, however, we come to inquire why it is that this beach species is the only representative of the genus in Hawaii and Tahiti, we are met with the possibility of its having been introduced by the aborigines. The tree is almost as useful to a Polynesian as the coco-nut palm, and it has been cultivated by him in some of the atoll-groups, as in the Marshall and in the Radack archipelagoes. In Chapter VII. good reasons are advanced for regarding it as an aboriginal introduction into Hawaii. When, therefore, we learn that in the group just named it extends from the sea-coast to nearly 2,000 feet above the sea, that in Samoa it may at times be found at a similar elevation though usually restricted to the sea-border, and that in the same way in Tahiti and in Fiji it may leave the coast-region and extend into the heart of the islands, we are not inclined to look for any marked differentiation in its character. This indeed appears to be the case. Numerous varieties in different regions are referred to by Dr. Warburg; but the only important one in the Pacific islands here mentioned is a cultivated form from the Marshall Group. A variety from Hawaii is distinguished chiefly by the smaller size of its drupes.

Assuming, therefore, that the inland species are as a rule not derived from littoral species originally brought by the currents, and that no birds of our own time are in the habit of carrying the drupes of Pandanus to oceanic islands, in order to explain the distribution of such species we have to choose between the possibility of the agency of extinct Columbæ and birds similar in their habits and the alternative of a continental connection. Dr. Warburg, who says but little of the mode of dispersal of Pandanus drupes, regards the genus as having now two centres,

one in the East African islands (Madagascar, the Mascarenes, and the Seychelles), and the other in Papuasia (New Guinea, extending doubtless to New Caledonia). My readers will recall to their minds that zoologists have at times felt bound to postulate a continent in both the centres of the genus Pandanus. There is the well-known Lemuria of the Indian Ocean, and then we have in the Western Pacific Forbes' Antipodea and Hedley's Melanesian Plateau.

Before, however, we accept the indications of the distribution of Pandanus as favouring a continental hypothesis for either area it is essential to exclude the agency of the extinct Aves. In this connection it is of prime importance to notice that the Mascarene Islands are remarkable, when contrasted with all other oceanic islands, not only for the predominance of peculiar species of Pandanus, but also as having been the home of extinct Columbæ like the dodo and the solitaire. The dodo's habit of swallowing pebbles of the size of a nutmeg (*Encyclopædia Britannica*, vii., 322), and the solitaire's inclination for swallowing stones as large as a hen's egg (*Birds*, by A. H. Evans, p. 331), doubtless represent, as explained below, a capacity for the dispersal of large fruits and seeds that would be regarded as "impossible" for distribution by birds now. It is quite possible that at some time the ancestors of these birds possessed the powers of flight now owned by the Nicobar pigeon, in the gizzard of which, in the Solomon Islands, I found quartz pebbles half an inch across (*Solomon Islands*, p. 324). In the work just quoted I refer on page 325 to the observation of Messrs. Chalmers and Gill that the Goura pigeon of New Guinea usually carries a good-sized pebble in its gizzard. We do not, however, seem to possess any record of extinct Columbæ in the tropical islands of the Western Pacific. The nearly extinct Didunculus of Samoa apparently prefers berries and soft fruits. Dr. Reinecke says that it especially favours the berries of Cananga odorata, the seeds of which are not over a third of an inch (8 mm.) in length.

It would appear from Mr. Hamilton's note in the *Transactions and Proceedings of the New Zealand Institute* (vol. 24) that the extinct Struthious birds of New Zealand, as in the case of the moa, carried crop-stones sometimes as large as a pigeon's egg. These pebbles are, of course, swallowed by birds to enable them to crush the hard seeds, and "stones" of fleshy fruits, on which they feed. In the Solomon Islands I noticed that the Nicobar pigeon was able in this way to crack the seeds of Adenanthera pavonina, which

for their fracture require a blow with a hammer. The implication is that the extinct Columbæ were able to transport to oceanic groups seeds and "stones" which no existing pigeon could now carry over a tract of ocean. I am inclined to extend this view also to extinct Struthious birds, and to suppose that they were able, like the cassowary (see page 152), to fly across tracts of sea in ages gone by. Though such an agency would come under discussion in connection with the floras of New Zealand and Madagascar, we have no evidence to show that birds of this family ever reached the tropical islands of the open Pacific.

The Megapodidæ of the Western Pacific are a family of birds that suggest themselves in this connection. Their distribution corresponds with that of Pandanus in the Western Pacific, excepting the littoral species; and like Pandanus the Megapodes have "differentiated" in every group. The limited powers of flight possessed by existing species would unfit them for crossing wide tracts of sea; but the parent form or forms of all these species must have been able to traverse broad tracts of ocean. These birds subsist on fallen fruits, seeds, &c.; but I have no data relating to them as seed-dispersers.

It is evident from the endemic character of most of the species of Pandanus in oceanic islands that, except with a few widely-spread littoral species, the dispersal of the genus has been for ages suspended. Whether the explanation is to be found in the isolation and differentiation of the extinct Columbæ of the Mascarene Islands, where the endemic species of Pandanus are most numerous, has yet to be established. It seems to offer the only way out of the difficulty, unless we accept the old view concerned with the continent of Lemuria.

Barringtonia.

There are two littoral species of this genus in the Pacific, B. speciosa and B. racemosa, both widely spread over the Old World, but only the first is generally distributed over the Polynesian region reaching east to Ducie Island, whilst the second does not extend east of Fiji and Samoa. With the exception of one or two inland species in Fiji and Samoa no inland species have been recorded from the groups of the open Pacific, and the genus is not represented at all in Hawaii. If it were not for a suspicion that the aborigines may have aided in the distribution of the inland species, the advocate of the previous continental connections of the islands

of the Western Pacific would receive from their occurrence in these islands considerable support for his views. The fruits of the inland Fijian species are large, the smallest being three inches in length ; and the agency of birds seems to be out of the question.

The fruits of the littoral species possess dry buoyant husks that enable them to be carried by the currents over wide tracts of ocean. Those of the Fijian inland species display only a trace of these buoyant coverings and the floating power is much diminished or absent altogether. These inland species are two or three in number. One of them, described as a new species by Seemann under the name of B. edulis, has edible kernels and is sometimes cultivated. A species that I found growing in the plantations of the Solomon Islanders in Bougainville Straits may be near the Fijian tree just named (*Solomon Islands*, pp. 85, 297). Its kernels are edible ; and I may add that the Solomon Islanders cultivate other species with edible fruits. We cannot, therefore, exclude the agency of the aborigines in the distribution of the inland species of this genus. Horne found an undescribed species in Fiji, which may be that which I found on the slopes of Mount Seatura in Vanua Levu, as described in Note 50 ; and it is quite possible that it was originally a cultivated tree, though not necessarily within the memory of the later generations of the aborigines.

This retrocession to the wild state of cultivated plants and the resulting production of apparently new species is a point on which Dr. Beccari lays considerable stress in the English edition of his book on the Great Forests of Borneo. He takes the case of Nephelium and other fruit-trees and shows how in old clearings, long since abandoned, they have undergone singular alteration in characters. For these reasons, therefore, Barringtonia can scarcely be regarded as offering in its inland species unequivocal evidence of a previous continental condition of the islands of the Western Pacific. Nor, as shown in Note 50, should we be justified in establishing a genetic connection between the inland and coast species ; but a great deal of research is needed before we can handle the numerous interesting problems connected with the genus ; and indeed it cannot be said that the specific limits of the inland Polynesian trees have been definitely determined, or the species themselves diagnosed.

SECTION V.

In this section are included those genera where within the same genus some inland species have been derived from the coast species whilst others have been originally brought by birds. Guettarda alone belongs here. In this genus we find, as is so frequently the case, a littoral tree (G. speciosa) widely spread in the Old World and ranging over the whole tropical Pacific as far east as Pitcairn and Elizabeth islands, but absent from Hawaii. Here also as with Pandanus it is only in the Western Pacific that we find inland endemic species so distinct in character from the littoral tree that they may be regarded as of independent origin.

Since, however, there is an inland form of the coast species in Tahiti (Guettarda speciosa, var. tahitensis) which, according to Drake del Castillo, is distinguished only by its more rounded leaves and by the more marked pubescence of the under leaf-surfaces, we evidently have there an inland species in process of development from the littoral species. This inland tree is found at elevations as great as 600 metres or almost 2,000 feet above the sea; and indeed if we follow Nadeaud the specific differentiation is complete. However, there is no doubt raised as to its close affinity to the beach tree; and we are almost compelled for another reason to regard it as a derivative of the shore species, because, as pointed out in Chapter XXVII., there are very few inland plants in the Tahitian flora possessing fruits as large as those of Guettarda that owe their presence in those islands to frugivorous birds.

Of the two inland species of the genus found in Fiji, G. inconspicua and G. vitiensis, it may at once be said that, as indicated in Dr. Seemann's work, their characters are far from suggesting any connection in origin with G. speciosa, the shore-species, the inland and littoral plants belonging to different sections of the genus. In their case we can only look to the frugivorous bird for the explanation of their existence in the group. The fruits would be probably small; and in this connection it is to be noted that Mr. H. N. Ridley in his paper on the flora of Fernando Noronha evidently looks to birds to account for the presence of a species of Guettarda on the island, a species not found elsewhere.

But another inland Fijian form of Guettarda found by me in Vanua Levu at elevations of 1,000 to 1,400 feet above the sea, and dubbed by the natives with the name of the littoral tree (Mbua-mbua), corresponds in its close relation to G. speciosa with the

inland Tahitian form of that tree, and is to all appearance a derivative of it. It is chiefly distinguished by its thinner, more hairy leaves, which taper at each end and are not subcordate at the base as is often the case with the leaves of G. speciosa. The coverings of the fruit are less fibrous and the putamen is not so deeply notched or grooved. The difference also extends to the buoyancy of the fruits in accordance with the principle laid down in Chapter II. Whilst those of G. speciosa float for many months and are of common occurrence amongst the stranded drift of tropical beaches, as for instance in the Keeling Islands, in the Solomon Group, and in Fiji, those of the inland species float only for a few weeks, their softer coverings decaying more rapidly in sea-water.

We seem therefore to have had two principles at work in Fiji in determining the origin of the inland species of Guettarda. Whilst in one case the inland species is so sharply distinguished from the coast species as to require the independent agency of frugivorous birds to explain its presence, in the other the inland form, as in the instance also of the Tahitian variety, is so much akin to it that the probability of derivation from it is very great.

SECTION VI.

In this section are contained genera possessing littoral species restricted to the Western Pacific islands, and dispersed by birds, but having little or no capacity for dispersal by the currents. They are regarded as derived from the inland species of the genus in the western part of the Pacific, and as distributed from thence over the islands in that part of the ocean. We are here only concerned with Fiji, Tonga, and Samoa and the neighbouring islands. The genera Eugenia, Drymispermum, and Acacia are here comprised.

The genus Eugenia, though essentially inland in its station, is apt to lend species to the beach-flora in different parts of the tropics. Such species, being dispersed by frugivorous birds and other animals, and possessing but slight capacity for distribution by the currents, are usually restricted in their areas. Thus, Schimper (p. 118) names two or three species, including E. javanica, as amongst the Indo-Malayan strand-flora. Ridley notices that E. grandis is a common sea-shore tree in the Malay peninsula; and the author observed two littoral trees of the genus

in the islands of Bougainville Straits in the Solomon Group, the fruits of one of them that flourished in the interior of the coral islets being found in the crops of fruit-pigeons. So also in Fiji, some of the inland species, as E. rariflora, appear at times amongst the strand vegetation and in the coral islets. There is, however, one Fijian species found also in Samoa and Tonga that is a characteristic beach tree, namely E. richii (Gray), and it is more or less confined to that station. The fruits will float a fortnight in sea-water, which is nearly twice as long as most other Eugenia fruits will float; and it is quite possible that the currents may assist the pigeons in distributing the species. This genus is dealt with more in detail in Chapter XXVI.

The genus Drymispermum (Thymeleaceæ) comprises in the Western Pacific a number of species, of which two range over the groups of Fiji, Tonga, and Samoa, whilst some four or more are peculiar to Fiji. All are inland plants with the exception of D. Burnettianum, a characteristic littoral shrub of these three groups. Its bright red drupes float only from five to ten days, even after some weeks of drying; and like those of the inland species they are well suited for dispersal by fruit-pigeons. This beach-plant may be regarded as probably an intruder in the strand-flora from the interior of one of the islands of the Western Pacific, whence birds, perhaps assisted a little by currents, have carried it to the neighbouring groups.

The very remarkable coast tree, Acacia laurifolia, alone represents its genus in the littoral flora of the Pacific islands. It is confined to the Western Pacific, having been found in New Caledonia, the New Hebrides, Fiji, Tonga, and Samoa; but it is doubtful whether it is truly indigenous in all these localities. Thus, in Samoa, though restricted to the coast districts, as we learn from Reinecke it seldom flowers, and according to that botanist it was probably introduced through cultivation. It is, however, evidently regarded by the Samoans as a tree of their group, as is shown in a curious legend, given by Dr. George Turner in his latest book on those islands, which I have quoted in my book on the Solomon Islands, p. 287. Both in Fiji and Samoa it bears the name "tatangia" or "tatania," whilst its hard wood was employed for various purposes, the leaves being used as spoons. The tree flowers and seeds freely on the Fijian beaches. The pods dry up on the plant, and do not dehisce, but are apt to break across between the seeds into article-like portions, the seeds being ultimately liberated by the decay of the pod or its fragments.

The seeds either sink at once or in the course of a day or two; whilst the pods or their fragments float at first in sea-water, but all are at the bottom in a week or less. With its absence of any apparent means of dispersal this small tree presents quite an anomaly in the strand-floras of the Western Pacific, and can only be regarded as a loan from the inland flora, though probably of a very ancient date, and perhaps going back like Acacia koa, the forest-tree of Hawaii, to some early epoch in the history of these islands.

The conclusions to be drawn from the discussion of the relations between the littoral and inland species of the same genus in the Pacific islands. (Chapters XIV., XV., XVI.)

In ten of the twenty-two genera here dealt with (Calophyllum, Hibiscus, Colubrina, Morinda, Scævola, Cordia, Ipomea, Vitex, Tacca, Casuarina) the shore and inland species have their own independent modes of dispersal, usually by currents in the case of coast plants, and by birds in that of inland plants; and the relations between the two are not such as to suggest a derivation of one from the other.

In six genera the inland species are regarded as derived from the littoral species. In two of them, as in Vigna and Premna, where the coast and inland species occur in the same group of islands and are connected by intermediate forms, there is direct evidence in favour of this conclusion; but such a development of inland species need not have taken place in every group, since in the instance of Premna it has apparently occurred only in the Western Pacific, and the inland and coast species have extended independently to the eastern groups through the agencies of birds and currents. . . . . In the other four genera (Canavalia, Erythrina, Sophora, Ochrosia) we have presented the so-called "Hawaiian difficulty," that group being alone concerned. Although these genera have no littoral species in Hawaii, they have inland species in those islands, which are in three genera endemic. Since these inland species have non-buoyant seeds or seedvessels, the transport of which by birds half-way across the Pacific Ocean is in the case of the first three genera unlikely and in the last impossible, it is assumed that they are all derived from original coast species with buoyant seeds or fruits, such as are widely distributed over the Pacific but are not now existing in Hawaii. This assumption, in the instance of the Leguminosæ, to which the first three genera

belong, derives support from the singular fact in the distribution of the order pointed out by Mr. Hemsley, that it is wanting in many oceanic islands where there is no littoral flora.

In one genus, Guettarda, the inland species are regarded as having been sometimes developed independently of the coast species, and as at other times derived from it, both principles having been at work in Fiji and only the last in Tahiti.

In two genera, Pandanus and Barringtonia, which represent the "Fijian difficulty," there is no reason on grounds of affinity to connect the inland with the coast species; and since the agency of existing birds is improbable in the first genus and out of the question in the second, whilst the operation of the currents is excluded for the inland species of both genera, it is assumed that we must either appeal to the agency of extinct birds, such as those of the Mascarene Islands, or we must fall back on the hypothesis of a continental connection. In the instance of Barringtonia it is also possible that some of the inland species may have been derived from species spread through cultivation.

Lastly, in three genera (Eugenia, Drymispermum, Acacia) the coast species are viewed as derivatives of the inland flora in the Western Pacific, not necessarily in Fiji, but it may be in New Caledonia or in one of the other large groups. In this case the coast species of all three genera are either unfitted for dispersal by currents, or display the capacity only in a small degree.

We thus see that in only seven of these twenty-two genera, containing both littoral and inland species in the Pacific islands, can it be argued from the standpoint of dispersal that the inland species are or may have been derived from the shore species; and in most instances the evidence is largely presumptive in its character. In three genera the reverse has been the case, and here the coast has borrowed from the inland flora. In twelve, or more than half of the genera, the shore and inland species have been evidently independent in their origin. It is accordingly apparent that in the Pacific the strand flora has lent more to the inland flora than it has borrowed from it; but with a large proportion of these coast genera no interchange has taken place. Two-thirds of the genera of the beach-plants have no inland species, and in their case the question of such a connection cannot be raised. With the remaining genera such a relation can be suggested in only two-fifths of the cases, or in about one-seventh of the total number of beach genera. Where a connection can be traced, it points more frequently to the derivation of the inland from the shore plant. Taking all the evidence

together, the beach flora presents itself in the Pacific as practically independent of the inland flora as regards its origin. It has received in these regions but few recruits from inland. It has yielded, except in Hawaii, but few recruits to the inland flora. In this ocean it bears the stamp of a high antiquity, though in the mass no doubt of more recent origin than the mangrove flora.

Yet, as I have remarked in different parts of this work, even with the beach genera possessing no inland species, considerable variety is displayed in the behaviour of the strand species. Thus, whilst some, like Pemphis acidula, Tournefortia argentea, and Triumfetta procumbens, rarely if ever leave the beach, others, like Heritiera littoralis and Excæcaria agallocha, find a home on the borders of the mangrove swamps, and one or two extend inland and take their place in the forests, either as trees (Afzelia bijuga) or as giant climbers (Entada scandens). Others again, like Cassytha filiformis, Cerbera Odollam, and Cycas circinalis, with a number of other beach-plants, may invade the interior of the island wherever arid plains or exposed scantily wooded districts offer conditions conformable to the xerophytic habit of the beach-plants.

It will thus be perceived that although the inland and coast floras of an island are in the mass distinct, the line of separation is by no means always well defined. Beach-plants are something more than salt-lovers in their ways. They are in the first place xerophilous, or, in other words, they will be equally at home in exposed situations away from the coast where the soil is dry and the rainfall scanty. Whenever these conditions are presented by the districts backing the coast, as we find for instance in the plains on the lee or dry sides of many a Pacific island, the shore-plants will often leave the beach and travel far inland.

Summary of Chapters XIV., XV., XVI.

(1) Though littoral floras are as a rule chiefly made up of two sets of plants, one brought through the agency of the currents from regions outside, and the other derived from the inland flora of the region concerned, the proportion of the two varies much amongst temperate and tropical strand-floras, the current-borne plants forming the majority in the tropics, and those from the inland flora of the region prevailing in the temperate zone.

(2) There is, therefore, far greater uniformity as a rule amongst tropical strand-floras than in the temperate zone, since in temperate latitudes the prevailing constituents of the strand flora vary with

the inland flora of every region, whilst in the tropics the predominant plants are those ranging far and wide on the shores of the warm regions of the globe.

(3) Regarding the tropical strand-flora as comprising two formations, that of the beach and that of the mangrove swamp, the last, which is the older of the two, may, it is suggested, be viewed as the remnant of an ancient flora widely spread over the lower levels and coastal regions of the globe, during an age when, in a warm atmosphere charged with watery vapour and heavy with mist and cloud, vivipary or germination on the plant was not the exception but the rule.

(4) But it is contended that even in the beach formation some of the plants may date back to this age of vivipary, as is indicated by the anomalous seed-structures of some of the genera, such as Barringtonia, which seem to indicate a lost viviparous habit.

(5) Since the beach formation of the islands of the tropical Pacific is largely formed of plants ranging over great areas in the tropics, there is no reason to expect that it owes much to recruits from the inland floras of this region. The discussion, therefore, of the relation between the littoral and inland floras is mainly concerned with the possible origin of inland from coast plants in these islands.

(6) Yet there are numerous cases of genera possessing both coast and inland species that are of peculiar interest in determining the true relation between the beach and inland floras.

(7) As the result of a detailed discussion of these genera, the conclusion is formed that the beach and inland floras have been in the main developed on independent lines, the beach flora receiving from the inland flora but few recruits, and except in Hawaii yielding but few plants to the inland flora. Only a third of the genera of the beach flora have also inland species, and in only a few of these genera, or about a seventh of the whole beach flora, can any question of a connection between coast and inland species of the same genus be raised.

(8) Two special difficulties arise in this discussion. The first is the "Hawaiian difficulty," which is more particularly concerned with genera of the orders Leguminosæ and Apocynaceæ. Here are genera which possess both inland and littoral species, but only the first occur in Hawaii. In the absence of any likely means of dispersal, whether by currents or by birds, it is assumed that the inland species are derived from shore plants, originally brought

by the currents, that have since disappeared, a view supported by the fact that Leguminosæ are wanting in oceanic islands where there is no littoral flora. The second is the "Fijian difficulty" which is best represented by Pandanus. From our inability to regard the inland species as derivatives of the coast species, or to supply them with a means of dispersal, we are compelled to regard them either as having been a part of the original continental flora of Fiji or as owing their existence there to the agency of extinct birds having the habits of the Nicobar pigeon and of the extinct Columbæ of the Mascarene Islands. Since the Mascarene Islands are noted not only for their extinct Columbæ but also for their number of peculiar species of Pandanus, the implication seems to lie against the continental view. The subject, however, awaits further investigation. In the Western Pacific the possible agency of the parent forms of the existing species of Megapodidæ is worthy of attention. Like the Columbæ and Pandanus in the Mascarene Islands, the Megapodes and Pandanus have "differentiated" together in the Western Pacific.

(9) The general view of the independent origin of the beach and inland floras of the Pacific islands is supported by the large number of genera in the strand flora that only possess littoral species.

(10) Such shore species, together with other strand plants, sometimes extend into the interior of an island, but only as a rule where the requisite conditions for a plant of xerophilous habit exist.

(11) Shore plants, it is pointed out, are xerophytes first and halophytes afterwards; and under certain conditions the purely xerophilous inclination prevails and the plants travel far inland.

CHAPTER XVII

THE STORIES OF AFZELIA BIJUGA, ENTADA SCANDENS, AND CÆSALPINIA BONDUCELLA

Afzelia bijuga.—The African home of the genus.—The double station of Afzelia bijuga, inland and at the coast.—The nature of the buoyancy of its seeds.—Summary relating to Afzelia bijuga.—Entada scandens.—Its station and distribution.—Darwin's opinion of the plant.—The dispersal of its seeds by the currents.—Summary relating to the plant.—Cæsalpinia bonducella and C. bonduc.—Their station and distribution.—Their characters in various Pacific groups.—The parents of inland species.—Their dispersal by the currents.—The germination of their seeds.—A dream of vivipary.—The causes of the seed-buoyancy.—Summary of results.

In this chapter we have a study of Leguminous strand plants that are of great interest. It can be safely said that the student of plant-dispersal in the Pacific will be brought into contact with the problems here involved wherever he goes.

AFZELIA BIJUGA (Gray).

This Old World tree, which belongs to the sub-family Cæsalpiniæ, is of great interest to the student of plant-dispersal. It is one of that large group of Indo-Malayan plants that extend into the Western Pacific, and give the prevailing character to the floras of such archipelagoes as that of Fiji. It is a large tree yielding a valuable timber used by the Fijians and Samoans for many purposes, such as for canoes, house-posts, clubs, kava bowls, &c., but it has not been recorded from the Tahitian region, and is unknown from Hawaii. In the fact of its being a littoral as well as an inland tree, it possesses a peculiar interest from the standpoint of plant-dispersal, and especially since this difference in station is associated with a difference in buoyancy, the seeds of the

inland trees usually sinking, whilst those of the coast trees usually float, and often for a period of months.

A glance at the distribution of the genus will enable us to appreciate some of the points that will be touched upon in the following discussion ; and it may he here remarked that the explanation of the distribution of these Leguminous trees will go far to make clear some of the most difficult points in plant-geography. Of the eleven species enumerated in the *Index Kewensis*, five belong to tropical Africa, occurring on both the east and west coasts as well as in the interior, three are confined to the mainland of tropical Asia, and two are peculiar to Malaya. In the last place we have the wide-ranging Afzelia bijuga, which, if it does not actually occur on the east coast of Africa, is found at all events in Madagascar and in the Seychelles, and is to be followed by the way of the Chagos Archipelago to the Malayan Islands and Queensland, and eastward to Fiji and Samoa.

The most suggestive feature in the distribution of the genus is to be seen in the frequent station of the species by rivers. We learn from Oliver's *Flora of Tropical Africa* that these trees find a home along river-courses on both sides of the continent, as on the banks of the Congo, the Niger, the rivers of Senegambia, and the Zambesi, the Zambesi species being found also on the shores of Lake Nyassa. Since tropical Africa possesses about half of the species, it would seem highly probable that it is the home of the genus, and that from the rain-forests in the heart of the continent rivers flowing east and west have borne the buoyant seeds of the wandering species to the coasts of the Atlantic and Pacific Oceans. The operation that I witnessed on a miniature scale in the case of a *species* of Entada (E. scandens) in the Isthmus of Panama, as described in a later page of this chapter, has been in progress through the ages with the *genus* of Afzelia in the breadth of the African continent. According to the principle illustrated by Afzelia bijuga in the forests of Fiji, the seeds of the African forest-trees would, as a rule, possess no floating power ; but now and then in the lapse of long periods of time buoyancy in some species would be developed, and such species would ultimately, through their buoyant seeds, find their station along the lower courses of the rivers.

To sustain this view it is not necessary that continuous rain-forests should now clothe the elevated regions in the interior of tropical Africa ; but it is requisite that there should be sometimes a generic similarity between the plants of the East African and West

African rain-forests; and it is evident that this is the case. Pechuel-Lösche, as quoted by Schimper (*Plant-Geography*, p. 299), describes the rain-forest on the Loango coast as covering the mountain ranges and as extending to the river-plains. In such a locality the operation would be rapid. In advancing this hypothesis I am referring to the possibility, however, of such an operation having effected the distribution of Afzelia in tropical Africa in the past rather than in the present. I would suggest that botanists in other habitats of the genus, as for instance in Queensland, might put it to the test of observation and experiment.

The interest that attaches itself to the story of the genus in its African home may be extended to the species that forms its outpost in the Pacific, and we shall see there a littoral species that doubtless had its home in the interior of a continent endeavouring, with a considerable measure of success, to become again an inland plant. Horne (p. 112), who was familiar with Afzelia bijuga at the two extremes of its range, namely, in the Mascarene Islands and in Fiji, speaks of it as characteristic of the shores of tropical regions; and Schimper, who includes it in the Indo-Malayan strand-flora, implies that it is more or less exclusively confined to the coast and its immediate vicinity (pages 121, 191–2). In the Seychelles, according to Mr. Button, this tree attains gigantic dimensions on the sandy flats. Still larger trees occur in the coral islands of the Chagos Archipelago; but in the atoll of Diego Garcia, as we learn from Mr. Bourne, it is almost extinct only some four or five trees existing there about twenty years ago, the increase of the tree being prevented through the destruction of the fallen seeds by the rats (*Journ. Linn. Soc. Bot.*, vol. 22, 1887).

Afzelia bijuga may, therefore, be safely regarded as a littoral tree. We shall now see the importance of this conclusion when we come to consider its station in the Pacific islands, where it grows both inland and at the coast, and we have to decide to which station we must assign the priority. Speaking of its occurrence in Fiji, Dr. Seemann says it is "common in the forests all over Viti," but makes no allusion to it as a littoral tree either in Fiji or elsewhere. On the other hand, Mr. Horne (p. 112) describes it as "generally growing on the shore or sandy beaches, and in rocky clefts, and by the sides of streams in the interior of Viti Levu and Vanua Levu." It was on or near the coast in Fiji that the present writer was most familiar with this tree, sometimes bordering the sandy beach, at other times growing behind the

mangrove-belt, or again thriving in the half sandy and half swampy soil of some low islet off the mouth of the Rewa. Especially is it to be found on those parts of the coast where the hill-slopes descend rapidly to the beach, or where some lofty spur from the mountains of the interior reaches the shore. It is also not uncommon on the banks of rivers both in their lower and upper courses. But it is as a forest-tree of the interior that it is most valued by both the white men and the natives on account of the superior quality of its timber in that station. There, far removed from stream or river, the Vesi, as the Fijians name Afzelia bijuga, takes its place amongst the lofty forest-trees, such as the Ndamanu (Calophyllum), the Ndakua (Dammara), and the Wathi-wathi (Sterculia). It is not often that one finds a tree in these islands that, like the Vesi, is able to make its home in almost any station, excepting, however, the "talasinga" or "sun-burnt" regions of the plains. Wherever tall trees grow gregariously in Vanua Levu, one will probably find Afzelia bijuga, whether beside a sandy beach, or bordering a swamp, or on a river's bank, or on some rocky declivity, or on the great forest-clad mountain-slopes and plateaux of the interior. No doubt the same diversity of station is displayed in Samoa, where, according to Dr. Reinecke, the tree is most frequent in the "coast-bush."

From the variety in station it might be expected that corresponding variations in character would be found. There are differences, such as in the quality of the timber and in the size of the seeds between coast and inland trees; but the most important distinction in connection with the study of the dispersal of the species is to be found in the circumstance that whilst the seeds of the coast trees are, as a rule, buoyant, and often float for months, those of the inland trees usually sink, even after being kept for three or four years. I made a considerable number of experiments on the buoyancy of the seeds of this tree in Vanua Levu, and found that with the coast trees, as a rule, either all the seeds or the majority of them floated in sea-water, whilst with the inland trees either all of them or the majority of them sank. The buoyant seeds are able in most cases to float for a long time. Thus, in one experiment half were afloat after two months, and in another half were afloat after five months. It is probable that several of the exceptions, where inland seeds float, will prove to be connected with an inland station by a river. (I experimented on eight sets of seeds of coast trees from eight different localities, and found 70 to be the mean percentage of buoyant seeds. In the same way, four sets of

seeds from four different inland localities gave 13 as the mean percentage of buoyant seeds.)

As in the case of Entada scandens, there is a rather fine adjustment between the mean specific weight of seeds and the density of water. If we place a number of the buoyant seeds in sea-water and begin to lower the density, some of the seeds will at once commence to float heavily and afterwards sink; and when the density has been lowered to approximately that of fresh water, usually about a third will be found at the bottom of the vessel. Out of 100 coast seeds, 70 will, as a rule, float in the sea and about 47 in the river; whilst of the same number of inland seeds, 13 on the average will float in sea-water and 8 or 9 in fresh water. The bearing of facts of this kind is especially discussed in Chapter X.

Coming to the causes of the floating-power of the seeds, we find that with the buoyant seeds the kernel floats, whilst with the non-buoyant seeds it sinks, the seed-tests in neither case possessing any floating-power. In this respect, therefore, the seeds of Afzelia bijuga belong, with the seeds of some other Leguminous littoral plants of the Pacific islands, such as Canavalia obtusifolia, Erythrina indica, and Sophora tomentosa, to the second section of the second non-adaptive group of buoyant seeds (page 107). But though we can in a measure explain the cause of the buoyancy, we are still ignorant of the manner in which the difference in the buoyant behaviour of coast and inland seeds has been brought about. It is possible that this may be connected with another difference between the coast and inland seeds, the latter being markedly smaller, and it is noteworthy that in my experiments the smaller seeds were generally those that sank. (Whilst the inland seeds averaged between $\frac{8}{10}$ and 1 inch, or 20 to 25 mm., in greatest diameter, 12 to 16 being required to make an ounce, the coast seeds measured 1 to $1\frac{2}{10}$ inch, or 25 to 30 mm., and only 10 or 11 were needed to weigh an ounce.)

There can be no question that the seeds are at times transported by the currents over wide tracts of sea, and this no doubt explains the occurrence of Afzelia bijuga in oceanic islands. They may be usually seen lying free in numbers on the ground beneath the tree or else still inclosed in the fallen dehiscing and decaying pods; and they might be swept sometimes into the sea or washed down into an adjacent stream. They thus came under my notice amongst the stranded beach drift at the mouths of estuaries in Fiji. But it is remarkable that the seeds have not apparently been recorded from the beach drift of other tropical regions. Penzig

does not note them amongst the seeds stranded on the shores of Krakatoa. They did not occur amongst my collections from the beaches of Keeling Atoll or of the south coast of Java; nor does Schimper mention them amongst the drift of the Java Sea. In the *Botany of the "Challenger" Expedition* the species is not even referred to in any connection. Although, however, the capacity of these seeds for dispersal by currents is for the first time established by me, their fitness in this respect was surmised by Schimper (p. 191), when he placed the species in his list of tropical shore plants evidently distributed by the currents.

It will thus be gathered that we have yet much to learn in this matter; and I would recommend any resident in the tropics to take up this subject. When indeed we remember the fine adjustment existing between the specific weight of the seeds and the density of water, and recall the unknown factor determining the difference in buoyancy between the kernels of coast and inland seeds, we can understand how under particular conditions in certain portions of its range the seeds of Afzelia bijuga may perhaps never possess any floating power. It would seem, in fact, that the seeds are much more buoyant in the Western Pacific than they are in the Java Sea; or it may be that the tree is much less frequent; or that the stranded seeds are soon destroyed by crabs, such as is the fate of much seed-drift on the Keeling beaches; or lastly that, as in Diego Garcia, rats in destroying the fallen seeds are bringing about the extermination of the species.

Summary relating to Afzelia bijuga.

(1) Assuming that the genus has its home in the African continent, and that the species have frequently a riverside station, it is argued that the distribution of the genus on both sides of that continent can only be explained by its dispersal by rivers from a centre in the interior.

(2) Afzelia bijuga, a widely distributed shore tree of tropical Asia, occurs in Fiji both at the coast and in the inland forests.

(3) This double station is associated *inter alia* with a different buoyant behaviour of the seeds, those of the coast trees usually floating for long periods, whilst those from inland generally sink.

(4) There can be no doubt that this widely ranging littoral tree has been dispersed by the currents; but the specific weight of the

coast seeds is on the average but slightly less than that of sea-water; and it is to this fine adjustment, always liable to be disturbed by variations in the environment, that the irregularities in the distribution of the species are to be attributed.

Entada scandens (Benth.).

The story of Entada scandens, a plant familiar to many of my readers under the name of the Queensland Bean, is a story of three continents, Africa, Asia, and America. From the point of view of its dispersal two features at once attract attention in the case of this giant-climber; in the first place its wide distribution over the tropics of the Old and New Worlds, and in the second place the great capacity of its large seeds, often two inches across, for dispersal by the currents. But before discussing these matters it will be necessary to glance at the distribution of the genus, since much light will thereby be thrown on some of the numerous difficult points affecting this extremely interesting tropical plant. Of the thirteen species enumerated in the *Index Kewensis*, seven are African, three are American, one is Burmese, one hails from Madagascar, and, lastly, there is the world-ranging Entada scandens, concerning whose home botanists are not agreed. Most of the species would seem to be inland plants, whilst Entada scandens thrives both inland and at the coast. Africa would thus appear to be, as with Afzelia, the principal home of the genus, but with America as a subsidiary centre.

In many points Entada scandens presents a parallel to Cæsalpinia bonducella, another Leguminous tropical plant which occurs also at the coast and inland. But since they both owe their wide distribution to their littoral station, it will be as coast plants that they will be most properly considered in this and the following chapter. Yet if the student were to regard the distribution of these two plants in a continental region as in India, where they extend inland to the Himalayas, he might fail to discern their true station. To accurately gauge the matter of their station, it is necessary for him to look at the plants as they occur in the islands of the Pacific. There he will first see the stranding of the seeds on a shore by the currents, then their germination and their development into giant-climbers over the littoral trees or into straggling bushes on the beach; and afterwards he will observe the plants of both species extending inland, and in these three stages he will

learn their history in the Pacific ; but a history, it may be observed, that in this region represents their efforts to return to an inland station, such as they once possessed in their birthplace in some distant region of the globe.

Dealing first with the station of Entada scandens, it may be remarked, as Dr. Seemann points out, that in Fiji it is most characteristic of the mangrove-formation. But it also occurs amongst the trees at the back of the mangrove swamp, on the beaches, on the banks of the estuaries, and at the edge of the inland forests where they border on the plains. Sometimes in the company of Derris uliginosa it grows not as a climber, but as a prostrate plant on the sandy beaches ; and here, not being able to assume its normal habit of a climber, it does not seed. It is to be found at times far inland in open-wooded districts. Thus in Vanua Levu I found it growing in the Mbua district four miles inland, and 1,400 feet above the sea. Reinecke speaks of it in Samoa only in connection with the "urwald," or primeval forest. Cheeseman describes it as most abundant in the interior of Rarotonga, covering the trees with a wide-spreading canopy of green. In the Malayan region Schimper refers to it as a plant of the beach-tree formation. In Ecuador and on the Panama Isthmus it grows not only at the coast, but also on the hill-slopes in the rear of the mangrove-belt.

With reference to the distribution of the plant, it may be remarked that, although it is found all round the tropics and possesses great capacity for dispersal by currents, there are certain difficulties in explaining its wide area and in accounting for its very peculiar distribution in the Pacific islands. It was doubtless in allusion to some of these difficulties that Mr. Darwin, in a letter to Sir Joseph Hooker, remarked : "Entada is a beast " (*More Letters*, &c., i, 93). There is at first the question of the identity of the species in the Old and New Worlds. It is here assumed that it is the same in both hemispheres ; but it must not be forgotten that the identity is "not beyond doubt" (*Bot. Chall. Exped.* iv, 147).

Then there is the difficulty connected with its occurrence on both coasts of tropical America. In this respect it is at one with some other littoral plants, like Ipomea pes capræ, as well as with the plants of the mangrove formation, as is pointed out in Chapter VIII. Whilst with the mangroves it is necessary to assume that they antedate the land connection between North and South America, this is not requisite in the case of Entada scandens,

since it grows in the interior of the Panama Isthmus, and rivers on the north and south sides now carry its seeds seaward from the same "divide" to the Atlantic and Pacific Oceans, as described in Chapter XXXII.

But, as I have also shown in Chapter VIII, America forms with the West Coast of Africa a region characterised by the same tropical littoral flora. This region, on account of the arrangement of the currents, stands in a very peculiar relation with the Asiatic region, which comprises the rest of the tropics, and to a great extent possesses its own peculiar strand-flora. There are a few littoral plants, like Entada scandens, Canavalia obtusifolia, Sophora tomentosa, and Ipomea pes capræ that occur in both areas; but the large majority are confined to one or other of them, either to the American region, including the African West Coast, or to the Old World region, which includes the African East Coast. The American region gives to the Old World, but it can receive nothing in return. For this reason, it is argued, we are compelled to regard most, if not all, of the cosmopolitan tropical shore plants that are dispersed by the currents, such as those above named, as having their home in the American region. Entada scandens would, therefore, from this standpoint have its home in America.

Then, again, there is the difficulty connected with the distribution of this plant on both sides of tropical Africa. Though Oliver in his *Flora of Tropical Africa* mentions this species only in connection with the West Coast, he says it is probably widely spread in that continent, and he refers to a pod in the Kew Museum indistinctly labelled "Lake Ngami." I have not come upon any reference to its being a littoral plant on the East Coast, but since numerous littoral plants of tropical Asia are found on that coast its occurrence there or in the East African islands would be expected. However, as the genus has a centre in America, and as this species is regarded as of American birth, we are not called upon to employ the argument used in assigning to a non-American genus like Afzelia an African home. Since the African West Coast belongs to the American region of tropical shore plants dispersed by the currents, the presence of Entada scandens on that coast of Africa can be readily explained, whilst if it has reached the Malayan Archipelago from America by way of the Pacific, it would, by extending like many other Malayan coast-plants along the shores of the Indian Ocean, almost complete its circuit of the globe. It is in this fashion, I believe, that the other littoral plants, like Cæsalpinia bonducella, Canavalia obtusifolia, and Ipomea pes

capræ, that are found all round the tropics, have performed the circuit of the globe with America as their home.

One may remark in passing that the double home of the genus in America and the Old World, though offering a serious difficulty in plant geography, has no immediate bearing on the present mode of distribution of Entada scandens. Questions relating to the distribution of tropical shore-plants that are dispersed by the currents at first resolve themselves into considerations of the arrangement of the currents. Entada is not alone amongst the genera containing littoral species in having a home both in the Old and in the New World. Carapa is another instance, and additional cases might be cited.

The next peculiarity in the geographical range of this species is concerned with its irregular distribution in the archipelagoes of the tropical Pacific. Notwithstanding its great capacity for dispersal by the currents, although it occurs in all the groups of the Western Pacific as well as in the Cook Islands, it has not been recorded from the Society Islands, the Paumotus, the Marquesas, and Hawaii. Since, however, its seeds have been gathered by Mr. Arundel on the beaches of Flint Island, lying about six degrees north of Tahiti (*Bot. Chall.* iv, 302), it is not unlikely that it will be found growing in other parts of Eastern Polynesia south of the equator. One might have looked for an explanation of its rarity in Eastern Polynesia to the absence of mangrove swamps, in which, as in Fiji, it is sometimes most at home; but this is negatived by its abundance in Rarotonga, where mangrove swamps do not exist.

The dispersal of Entada scandens by the currents.—This plant offers one of the most conspicuous examples of the transport of seeds across oceans through the agency of the currents. In the pages of many botanical works, from the close of the 17th century onward, reference is made to the transport of its beans (often in association with those of Mucuna urens and Cæsalpinia bonducella) by the Gulf Stream or other currents across the Atlantic to St. Helena, the Azores, the west coast of Ireland, the Hebrides, the Orkney Islands, the coasts of Scandinavia, and even as far north as Nova Zembla (see Hemsley's *Bot. Chall. Exped.*; Sernander's *Skand. Veg. Spridningsbiologi*, &c.). That the seeds of Entada scandens retain their germinating capacity after this ocean-transport has been demonstrated not only by the germination of stranded seeds on the shores of St. Helena, but also by the germination when sown at Kew of seeds drifted to the Azores, as

well as by the results obtained by Lindman, who procured the germination of the seeds of this plant and of Mucuna urens that had been washed up on the Scandinavian beaches (see Sernander, pp. 7, 390).

One of the most interesting references to the conveyance by currents of these seeds to the coasts of Europe is to be found in Dr. Sernander's recent work on the modes of dispersal of the Scandinavian flora, where he sums up the results of Lindman's investigations respecting the Gulf Stream drift. The stranded seeds of Entada scandens, it appears, have been found all along the Norwegian coast, but occur most frequently north of the Söndmöre district. They have even been found in a sub-fossil condition in the peat-bogs of Tjörn on the Bohuslän coast in Sweden, having been originally stranded on a beach in that locality at some distant, but post-glacial, epoch. Few phenomena in plant-distribution are more suggestive than this ineffectual transport through the ages of these large tropical beans to coasts within the Arctic Circle. The seed, no longer under the care of the mother-plant, becomes a waif, exposed to the pitiless laws of the physical world which here prevail. It was not thus that the plant was reared, but it is in this haphazard fashion that its seeds are spread. The philosopher could unravel most of the tangled problems connected with present and past plant-dispersal, if he could follow the clue supplied by this stranded tropical seed on a Scandinavian beach.

It is a far jump from the North Cape to the coral islands of the Pacific and Indian Oceans ; yet it is within the area covered by the drifting Entada bean. The stranded seeds occur commonly on the Fijian beaches and on other islands of the South Pacific ; but I never found them in Hawaii. They were gathered by me on the shores of Keeling Atoll in the Indian Ocean, and on the south coast of Java. Penzig found on the Krakatoa beaches, in 1897, not only the stranded seed but the established plant. They came under my notice in numbers on the beaches of Ecuador and on the Pacific and Atlantic coasts of the Panama Isthmus ; and, as I learned, they are equally common on the other parts of the coasts of Central America. Not uncommonly these stranded seeds in various parts of the world are to be found incrusted with polyzoa and tubicular annelids, which afford proof of prolonged flotation in the sea. These seeds are also to be frequently noticed floating in the drift of the tropical estuaries. Thus they came under my observation afloat in numbers in the Fijian estuaries, in

the Guayaquil river, in the estuary of the Chagres at Colon, and in the mouth of a river on the Panama side of the isthmus.

The mode of liberation of the seeds is worthy of a passing remark. The huge pods, often several feet in length, ultimately break up into separate joints bearing the seeds. The joints may decay on the ground, and the seeds are thus freed; or not infrequently in a mangrove-swamp they fall at once into the water, and there they float, as may often be observed in Fijian rivers, until their decay sets free the seed.

The seeds of Entada scandens are often quoted, and justly so, as striking examples of the dispersal of seeds by currents. Yet in few plants could the nature or the structural cause of the buoyancy have so little claim to be considered as adaptive in its character. Quite half, and sometimes even the majority, of the seeds freshly liberated from the plant have no buoyancy at all. The mean specific weight of the seed is about that of sea-water, but markedly higher than that of fresh water; whilst the principal determining cause of the buoyancy is, as shown below, purely mechanical, and one that, whilst favouring the wide distribution of the species, could not be improved by or come within the scope of Natural Selection.

From experiments made in Fiji and Ecuador, it appears that at least 50 per cent., and often more than half, of the seeds when first liberated from the pod have no buoyancy in sea-water. Of those that float in sea-water, a proportion varying between one-third and one-half sink in fresh water, so that in the case of plants growing on the banks of a river only about one-fourth or one-third would be carried down to the sea. So fine is the adjustment of the specific weight of these seeds to the density of water, a subject discussed in its general bearings in Chapter X, that if one gathers a number of drift seeds on a beach, let it be in Fiji or in Ecuador, although, of course, all will float in the sea, only one-half or two-thirds will float in the neighbouring fresh-water stream. Those that float appear to be able to float almost indefinitely. This is sufficiently established by the transport of the seeds in a sound condition by the currents across the Atlantic, and by such evidence as the stranding of seeds incrusted with polyzoa and serpulæ on the beaches of Keeling Atoll. It has been also proved by the following experiment. Several years since, I placed a seed in a vessel of sea-water, where it still floated buoyantly in a perfectly sound condition twelve months afterwards.

With regard to the cause of the buoyancy, investigation shows that neither the seed tests nor the seed contents have any floating

power, the buoyancy arising from a large central cavity produced by the shrinking and bending outward of the cotyledons during the drying and hardening of the maturing seed (see figure in Chapter XII). With the seeds that sink, this cavity is, as a rule, reduced to small dimensions, and may be represented only by a narrow slit. In some cases, however, where the cotyledons are unusually thick and heavy, even a large central cavity will not give floating power to the seed. There is an indication in my experiments that seeds from inland plants that have matured their pods in the forests sink in a much greater proportion than seeds of coast plants, or of those growing on the banks of estuaries. This we might expect, since in the shade of the forests the drying process that accompanies the setting and final maturation of the seed would be less complete and the intercotyledonary cavity smaller than with the seeds matured in more exposed situations. This is a point, however, that requires further investigation.

It will thus be seen that in respect of buoyancy the seeds of Entada scandens are to be referred to the mechanical or non-adaptive group of buoyant seeds, described in Chapter XII, which comprises several other Leguminous strand-plants, including Cæsalpinia bonducella. I especially studied the various stages in the development of the buoyancy of seeds in this mechanical group in the case of the species of Cæsalpinia just named, and the description of the process as given under that plant will apply to all.

Summary relating to Entada scandens

(1) This plant, which has been distributed by the currents over the tropics of the globe, has its station in the mangrove swamp, on the beach, by the estuary, and in the inland forest.

(2) It is regarded as an American plant that has reached the shores of the Indian Ocean by crossing the Pacific, and the coast of West Africa by crossing the Atlantic.

(3) Its occurrence on both coasts of America is attributed to its having a focus of dispersal in the forests of Central America, from which its seeds have been transported by the rivers to the shores of the Atlantic and Pacific Oceans.

(4) Its irregular distribution in the Pacific islands, to wit, its absence from Hawaii and its rarity in the Tahitian region, is not to be easily explained, but it is more than likely that it will be subsequently recorded from other localities in Eastern Polynesia.

(5) Although the seeds offer a striking example of dispersal by currents, since they are to be found stranded on beaches over much of the globe, from within the Arctic Circle to the Coral Sea, in few plants could the character of the buoyancy and the structure connected with it have so little claim to be considered as adaptive in their nature. At least 50 per cent. of the seeds sink in sea-water, and the cause of the buoyancy of the other seeds is only to be connected with the large size of a cavity produced by the shrinking of the embryo within the seed tests during maturation.

CÆSALPINIA

This genus is represented in the tropics of both the Old and the New World by some eighty species of trees, shrubs, and climbers, some of which are noted for their dye-woods, and others for the beauty of their flowers. In the Pacific islands the botanist is only concerned with three widely distributed species, all more or less littoral in their station, and in great part dispersed by the currents, namely, Cæsalpinia nuga (Ait.), C. bonducella (Flem.), and C. bonduc (Roxb.).

With Cæsalpinia nuga we have little to do, since, although widely distributed in tropical Asia and the Malayan region, and reaching to both New Guinea and North Australia, it has not apparently penetrated into the Pacific further east than the Solomon and New Hebrides groups. I found it growing on the coasts of the larger islands of the Solomon group, but no observations were made on its mode of dispersal. However, as its seeds were identified at Kew (*Bot. Chall. Exped.* iv, 311) amongst my collections of stranded drift from those islands, it would appear to be to some degree dispersed by the currents, though since it does not extend far into the Pacific, its capacity for dispersal by this agency would seem to be limited. Schimper includes it among the strand-plants of the Indo-Malayan region.

It is with the other two species, Cæsalpinia bonducella and C. bonduc that we are especially interested. Their extremely hard, marble-like seeds at once attract attention, and when pale in colour they look not unlike quartz pebbles as they lie stranded on a beach. The prickly pods and the recurved prickles of the leaf-branches often make these plants provokingly evident to a stranger. Though usually to be characterised when growing on a beach as straggling shrubs, they will often climb trees when opportunities

occur, and they then display themselves as stout-stemmed climbers. I have seen one or other of them in the mangrove swamps of Fiji ascending the Bruguiera trees to a height of 30 feet and more, the stem quite bare below, but leafing and flowering in the tree-branches above.

From the standpoint of dispersal there are few more interesting plants in the Pacific islands; but their discussion raises several difficult questions, and it will be, therefore, requisite to treat them somewhat in detail. With regard first to the diagnostic characters between the species, it may be observed that, as a rule, they are sufficiently evident, such, for instance, as the number, size, and form of the leaflets, the presence or absence of foliaceous stipules, and the colour of the seeds, though, as shown below, the seed-colour in the case of Fijian plants does not always present a constant distinction. Yet as I found in Fiji the difference between the two species is not in all cases well pronounced, and intermediate forms occur, about which it is sometimes difficult to decide to which of the two species they should be assigned.

Mr. Hemsley remarks (*Bot. Chall. Exped.* iii, 114, 145, 300) that the two species have been often confused. I venture to think that this has been in some cases due to the occurrence of these intermediate forms. One has only to look at the different "distributions" given by botanists for C. bonduc, as indicated below, in order to suspect that the cause of confusion has been at times with the plants themselves. When in Fiji I paid a good deal of attention to this subject, and the results of the comparison of the foliage and seeds of the plants obtained from fourteen different localities in Vanua Levu are given below.

It will be seen in this table that I distinguish in Fiji three littoral forms and one inland or mountain variety, which may perhaps be a distinct species. Those of the strand include Cæsalpinia bonducella, C. bonduc, and an intermediate form. C. bonduc is typically distinguished by its large leaflets, by the absence of foliaceous stipules, and by its pale yellow seeds; whilst C. bonducella is similarly characterised by its small leaflets, its foliaceous stipules, and its lead-coloured or darkish grey seeds. But in the first species the colour of the seeds may often be yellow mixed with pale-grey, or almost white; whilst in the second species the seeds may be stained with brownish-yellow patches.

It seemed to me when examining fresh specimens in Hawaii and Fiji that the ultimate colour of the seed is a good deal determined by the degree of alteration of the original olive-green

colour of the immature seed. All gradations may be noticed from the olive-green of immaturity to the yellow, pale grey, and dirty white hues of the mature seeds of Cæsalpinia bonduc and to the lead or slate-colour of those of C. bonducella. It almost appeared as if the changes might be compared to the bleaching which a dark volcanic rock undergoes in the weathering process through the hydration and removal of the iron oxides.

Cæsalpinia in Fiji, Tahiti, and Hawaii.

Locality.	Species.	Foliaceous stipules.	Pairs of pinnæ.	Leaflets.			Seeds.	
				Pairs.	Length in inches.	Form.	Size in tenths of inch.	Colour.
Coast, Fiji	Bonducella	Present	8–9	9–11	1¼–1½	Oblong, obtuse mucronate: base rounded and inequilateral	6½–7½	Usually lead-colour with at times brownish-yellow patches.
	Bonduc	Absent	5–6	4–6	2½–5	Oblong, acuminate, mucronate, base rounded or subcordate	5½–6 6½–7½	Pale yellow Pale grey, sometimes mixed with yellow.
	Intermediate	Present	7–8	7–9	2–3	Oblong, obtuse mucronate, rounded at base; upper leaflets may be elliptical	6–7	Lead-colour or pale grey with brownish-yellow patches
Inland, Fiji	Mountain species	Present	5–6	9–10	1½–2¾	Lanceolate with long tapering aristate apex and rounded base	6	Yellowish or pale grey or mixed.
Coast, Tahiti	Bonducella	Present			½–1⅘	Oblong		
Inland, Tahiti	Bonduc	Absent		5–6		Oblong		
Inland, Hawaii	Bonducella		4–6	6–8	1⅗–2	Oblong, obtuse, not cordate at base	6–7	Lead-colour.

Note.—The characters of the Fijian plants are from my own observations. Drake del Castillo is quoted for Tahiti, and Hillebrand for Hawaii. Reinecke observes that the pods of C. bonducella in the inland forests have no prickles.

In Fiji all three coast forms may be found on the same beach, or they may exist apart. The large-leaved species (C. bonduc) appears to be much the most frequent in Vanua Levu; and the intermediate form is common enough to disturb the serenity of the observer's mind when he is anxious to diagnose rather than to collect cumbersome specimens. The mountain form, which came under my notice as a climber in the forest at an

elevation of 1,700 feet on the slopes of Koro-mbasanga in Vanua Levu, acquires from the lanceolate shape of its leaflets quite a character of its own, though it comes nearest to Cæsalpinia bonducella. Mountain forms also occur, as indicated in a later page, in the forests of Samoa and in Tahiti; but in the first-named group they are referred by Reinecke to C. bonducella, and in Tahiti by Drake del Castillo to C. bonduc. In the Samoan forests the inland plants possess pods deprived of the prickles that are so characteristic of the beach plants. Before one can pronounce definitely on the relation between the coast and inland forms in any of the groups, a thorough investigation of the connections between the two shore-species is needed. I am inclined to think that they will prove to belong to a single dimorphic (or perhaps polymorphic) species.

The distribution of Cæsalpinia bonducella and C. bonduc.—Botanists agree in giving C. bonducella a distribution around the tropics of the globe; but they are not at all unanimous with respect to the other species. According to Mr. Hemsley this species is by no means so universally dispersed as C. bonducella. It is unknown from Africa and Australia; but it is generally characteristic of tropical Asia and the Malay Archipelago. The same authority alludes to specimens in the Kew Herbarium from Florida and the West Indies (*Bot. Chall.* iv, 300). Drake del Castillo gives both species a range through the tropics, whilst Schimper seems in doubt about the occurrence of C. bonduc in the New World, and Mr. Burkill makes no allusion to its American habitat in his paper on the Tongan flora. The cause of this confusion is doubtless to be mainly attributed to the variation in characters of the plants, and to the occurrence of intermediate forms.

We should be scarcely consistent if we assumed that of two kindred shore-species dispersed by the currents one had its home in America and the other in the Old World. The same home must belong to both. According to the principle laid down in Chapter VIII, and referred to under Entada scandens, it is held that a strand-plant, with its home in Asia, on account of the arrangement of the currents could never reach the American continent, and that American shore-plants are for the most part native-born except those hailing from the African West Coast, which, however, lies within the American province of tropical strand-plants. From this standpoint Cæsalpinia bonducella would be regarded as now having its home in the New World, and since it is found on both the Pacific and Atlantic coasts of that continent (as well as on

both coasts of Africa), it is assumed, as with Entada scandens, that it has reached the African West Coast by crossing the Atlantic, and the African East Coast by way of the Pacific and Indian Oceans. The genus, I may remark, is distributed over the tropics of the eastern and western hemispheres.

As regards the general distribution of the two species in the Pacific islands, it would appear from the writings of Seemann, Hillebrand, Hemsley, Drake del Castillo, Reinecke, Cheeseman, and Burkill that with the exception of Hawaii and Samoa, where Cæsalpinia bonducella alone occurs, and of Rarotonga where C. bonduc alone is found, they are generally associated in the larger groups, as in Fiji, Tonga, Tahiti, and the Marquesas.

The station of Cæsalpinia bonducella and C. bonduc.—Both the species are to be regarded as littoral plants likely to stray inland. The first-named is described in the *Botany of the "Challenger" Expedition* as essentially a sea-side plant, though flourishing equally well inland, and in India extending to the Himalayas as far as Kumaon, and up to elevations of 2,500 feet. Schimper speaks of both species as characteristic of the Indo-Malayan strand-flora, and he quotes Kurz when referring to C. bonduc as a constituent of the beach-jungle of Pegu.

In the Pacific islands they are typically littoral in their station; but they may extend inland, and in one or two groups they are only known in their inland station. Dr. Seemann speaks of both species only in connection with the beaches in Fiji, and alludes to Cæsalpinia bonducella (p. 72) as sometimes climbing over the mangroves. In Vanua Levu both came under my notice on the beaches, and in their immediate vicinity, usually as straggling bushes, whilst at times they were to be observed climbing the mangroves at the borders of the adjacent swamp. In this island of the Fijis they do not, as a rule, stray far from the beach, and strange to say are not to be ranked amongst those seashore plants that frequent the "talasinga" regions or inland plains. Judging from the mountain form found in the forests of Koro-mbasanga, if they extend inland in Fiji they prefer the forests and become differentiated in character. In Tahiti, as we learn from Nadeaud and Drake del Castillo, C. bonducella occurs on the beach and extends inland to the mouths of the valleys; whilst C. bonduc is only recorded from the mountains at elevations of 600 to 700 metres (2,000 to 2,300 feet). Jouan is quoted by Mr. Hemsley as remarking that C. bonduc is as common in the Marquesas as brambles are in Europe (*Bot. Chall. Exped.* iii, 145). In Rarotonga, according to Cheeseman,

C. bonduc is restricted to the interior. In Samoa, as we are informed by Reinecke, C. bonducella is frequent both in the coast districts and in the mountain-forests. In the Samoan mountains the pods lose their prickles, and from this circumstance, as well as from the extremely widespread distribution of the species over the islands, the German botanist concludes that the plant has been for ages established in the group.

In Hawaii, Cæsalpinia bonducella, which alone occurs, rarely figures as a beach plant; but it is found, as Hillebrand observes, in the lower plains of all the islands. In the large island of Hawaii I found it not on the scanty beaches of the coast, but on the partly vegetated surface of the old lava-flows at distances varying usually between a hundred yards and a mile from the sea, but extending at times a few miles inland, and in one locality reaching an elevation of 2,000 feet above the sea. It was mostly observed by me on the dry side of the island, where, associated with Erythrina monosperma, the Cactus, and the Castor-Oil plant, it thrives in very arid localities, where the rainfall is only a few inches in the year. Farther inland, where the old lava-surfaces were more vegetated, it was associated with such shrubs as Osteomeles anthyllidifolia and Cyathodes tameiameiæ. Dr. Hillebrand, writing of a generation and more ago, says that in his time the plant was less common than formerly.

The Methods of Dispersal of Cæsalpinia bonducella and C. bonduc.—We come now to the modes of dispersal of these plants; and in so doing we have to choose between the agencies of birds and of currents. The seeds of C. bonducella are on the average $\frac{7}{10}$ of an inch (18 mm.) in diameter, whilst those of C. bonduc are rather smaller ($\frac{6}{10}$ of an inch or 15 mm.). As far as their size and character go, it would seem scarcely likely that birds could transport these seeds across an ocean; but our knowledge of the agency of birds is of a very imperfect nature. Yet their occasional dispersal by birds is not improbable. When I was in the Keeling Islands the residents informed me that the seeds of C. bonducella are sometimes found in the stomachs of sea-birds, such as frigate-birds and boobies. (See Note 59.)

However, it has long been known that the seeds of one or both of these species are carried great distances by the currents; but it is to be gathered that the older botanists, in alluding to this fact, more usually referred under the synonym of Guilandina bonduc to Cæsalpinia bonducella. De Candolle, loth to attach much importance to the effective transport of seeds by currents, was

compelled to admit this species in his scanty list of current-dispersed plants (see Note 33). For more than two centuries it has been known that the seeds of C. bonducella are carried in the Gulf Stream drift to the coast of Europe from the American side of the Atlantic; and ever since they were recorded by Sloane in 1696 as stranded in a fresh condition on the beaches of the Orkney Islands, they have been found washed up on other localities, as on the coasts of Ireland and of Scandinavia and on the shores of the islands of the Western Atlantic. According to Robert Brown, a plant was raised from a seed cast up on the west coast of Ireland; and with respect to Scandinavia, Dr. Sernander informs us that the seeds of Cæsalpinia bonducella, like those of Entada scandens and of Mucuna urens, are of frequent occurrence amongst the "Gulf Stream products" stranded on the Norwegian coasts. The seeds of this species are commonly washed ashore at St. Helena, and there are specimens in the Kew Museum that were stranded on Tristan da Cunha. (Those interested in the subject will find it discussed by Mr. Hemsley in the *Botany of the "Challenger" Expedition*, and also by Dr. Sernander in his recent work on Scandinavia.)

The seeds of Cæsalpinia bonducella have been also found stranded on beaches in other parts of the world. Thus Prof. Schimper found them in the beach-drift of the south coast of Java. Prof. Penzig noticed them amongst the stranded seeds of the Krakatoa beaches; but it does not appear that the plant had established itself up to the date of his visit in 1897, or fourteen years after the great eruption. They have been picked up on the other side of the Indian Ocean on the east shores of Africa (*Bot. Chall. Exped.* iv, 300). They came frequently under my notice stranded on the beaches of Keeling Atoll in the same ocean; and seedlings sprouting from the seeds were sometimes to be seen growing amongst the drift just above the high-tide level. The seeds of both C. bonducella and C. bonduc have been found also on the shores of Jamaica. Those of both species are not uncommon amongst the stranded drift of the Fijian beaches; but notwithstanding a careful search I found only a solitary seed of C. bonducella in the Hawaiian beach-drift, a circumstance explained below as arising from the usual non-buoyancy of Hawaiian seeds.

That the seeds of Cæsalpinia bonducella stranded on the coasts of an oceanic island are able to germinate and reproduce the plant is, of course, established by the distribution of the species; and we have just observed that the process was noticed by the author on

Keeling Atoll where the plant has found a home. It is to be noted that the plant collected by Darwin in this atoll was identified by Prof. Henslow as C. bonduc; but the plant observed by me was more like C. bonducella, and the stranded seeds collected by me were referred at Kew to this species. Some curious considerations arise from the fact that although, just as in the Keeling Islands, the plants of C. bonducella have evidently established themselves from drift seed in one locality in the Bermudas, they do not seem to have done so either on the shores of Krakatoa, or of St. Helena, where, although they are frequently washed ashore, Mr. Melliss never met with an instance of germination (see *Bot. Chall. Exped.* iv, 300, and Penzig). This is doubtless in part the result of the destructive efforts of the crabs, which, as I have shown in my paper on Keeling Atoll, nibble off the shoots of many germinating seeds in beach drift.

The readiness or non-readiness of seeds to germinate on a beach, and the nature of the conditions essential for the process, are matters that are directly concerned with their effective dispersal by currents. On account of the stony character of the seeds of these two species, it might be expected that germination would only take place under exceptional conditions. It should, however, be observed that the fine transverse striæ on their outer surface represent original fissures or cracks in the epidermis of the soft immature seed; and as such may be regarded as lines of weakness in the seed-tests. If a pod is opened before the seeds are mature, we find the seeds about twice the size of maturity, and so soft that they can be indented by the nail. The transverse striæ that mark the mature seed are displayed as indistinct cracks in the epidermis; and if the immature seed is exposed to the sun, in a few hours these cracks gape widely, and the seed has the grooved appearance of a top. If a pod opens prematurely on a plant, as sometimes happens, the immature seeds will be noticed with the epidermis scaling off. It is evident that the "setting" or the induration of the seed-coats and the final great contraction of the seed take place in the pod before dehiscence. From these remarks it would seem probable that seeds lying exposed to the fierce rays of the sun on a tropical beach would be liable to develop cracks along the old fissures, and that such cracks by permitting the entrance of moisture would favour germination.

My experiments show that high temperature under moist conditions will not of itself induce germination or in any way affect the seed. Thus in two sets of experiments, in 1890 and 1902, I

failed to induce the germination of seeds which, after floating a year in sea-water, were kept in moist soil at a high temperature. In one case a temperature varying from 80° to 110° F. was sustained for several weeks, and in the other experiment a temperature of 80° to 90° was kept up for five months. When, however, an incision was made into the epidermis, or the seed-coats were partially penetrated with a file, the seeds swelled up in a day or two, and in a few days began to germinate.

The rapid transformation of the stone-like seed into a softened, swollen, germinating mass ranks amongst the numerous little wonders of the plant world. The seed, in fact, assumes again the appearance of immaturity, and in so doing it suggests to us that the rest-stage exemplified in the hard, pebble-like seed is but an adaptation to general climatic conditions, and that in a region of great heat and humidity, where there are no seasons, and where the sun's rays are for ever screened off by mist and cloud, it could be dispensed with altogether. One of my Hawaiian dreams was to establish vivipary in Cæsalpinia bonducella by subjecting the maturing pod on the plant to very warm and humid conditions, my expectation being that the soft, swollen seed would at once proceed to germinate in the pod, and that the final process of setting, as indicated by the induration and contraction of the coats, or in other words the rest-stage, would be done away with. The dream, however, bore some fruits in enlarging my standpoint in the matter of vivipary, and I have referred to the subject in Chapter XXXI.

The seed-shell, about 1·5 mm. in thickness, consists of three coats: the outer skin very tough and waterproof; the inner skin seemingly permeable; and the intermediate layer of hard prismatic tissue, the "prismenschicht" of Schimper (p. 164). This middle layer absorbs water rapidly and in large quantity, so that if a fragment of the shell is placed in water it will be found after a day's soaking to be three times as thick as it was in the dry state. If one files a seed, or makes a small incision, so as to expose the middle layer without piercing the inner coat, and then places it in water, it will be noticed that the middle layer at once begins to absorb water; and within a couple of days the whole seed will swell and attain the size it possessed in the so-called immature condition. During the process the outer skin stretches, usually without rupturing; and all three coats, previously so hard that a heavy blow with a hammer is required to break the seed, become in a day or two soft enough to be easily cut with a knife. The

seeds thus treated swell in two days to three times their original size and increase their weight fourfold. Water finds its way to the nucleus or embryo partly through the dilated inner opening of the micropylar passage and partly through the inner skin. The nucleus then swells up into a fleshy mass, filling the seed-cavity, and in two or three days more germination begins.

I pass now to the discussion of the buoyancy of the seeds. Considering that both species occur in oceanic islands, and that the currents are active agents in transporting the seeds, their behaviour under experiment appears at first sight to be full of anomalies. Thus, it was ascertained at Kew (*Bot. Chall. Exped.* iv., 301), both with comparatively fresh and with older seeds, that those of Cæsalpinia bonducella floated in salt water, whilst those of C. bonduc sank; but in the record given of the experiment no mention is made of the original station of the parent plants; and it will be shown later on that the station of the plant, whether at the coast or inland, has an important determining influence on the buoyancy.

In Fiji I found that almost without exception the seeds of littoral plants of Cæsalpinia bonducella floated both in sea-water and in fresh water. On the other hand, in Hawaii the seeds of this species, obtained from three typical localities removed inland from the beach, sank without exception, even after drying for several months; and the only buoyant seed noted in these islands was a solitary seed collected from the beach drift. In Hawaii, however, as before remarked, the species is not strictly a littoral plant, occurring as it does in the lower levels, but not necessarily in the vicinity of the coast. In the case of seeds of littoral plants of C. bonduc in Fiji, I found that sometimes all floated in sea-water and sometimes only a portion of them, whilst their specific weight was on the whole rather greater than that of the seeds of the other species. Thus, in one experiment half the seeds floated in sea-water and a quarter in fresh water, whilst with seeds from another locality 90 per cent. of the seeds floated in sea-water and 80 per cent. in fresh-water; and in a third set of seeds all floated in both waters.

The above experiments on Fijian seeds all relate to littoral plants. In the instance, however, of the inland species from the mountains of Vanua Levu, all the seeds sank in sea-water, even after being kept for five years. If we follow the indications of these several experiments we shall find that Cæsalpinia presents another illustration of the general principle established in Chapter

II that the seeds of inland plants sink and those of coast plants float.

My data, therefore, show that with the seeds of Cæsalpinia buoyancy goes with station and not necessarily with species. It is probable, therefore, that with the two widespread species, C. bonducella and C. bonduc, varying results will be obtained with seeds from different localities, whether insular or continental, according to the original station. The typically buoyant seeds of the former species may, as we have seen in Hawaii, lose their floating powers when they grow inland; and the seeds of an inland species from the mountains of Fiji sink at once. It is essential in interpreting the results of experiments on the seeds of these plants to be acquainted with the stations; and in this respect those of the Tahitian plants may be regarded as probable test cases. We have seen that in Tahiti, C. bonduc is an inland plant, and C. bonducella usually a beach plant; and I have no doubt that experiments in that island on the seeds of these two species from the particular stations just referred to will give results in agreement with the principle here laid down.

With reference to the duration of the floating powers of these seeds it may be observed that a seed of Cæsalpinia bonducella, originally found stranded on the beaches of Keeling Atoll, floated after a year in sea-water as buoyantly as at the commencement of the experiment. Seeds of Fijian littoral plants of both C. bonducella and C. bonduc floated in my experiments after two and a half years' immersion in sea-water, showing no change whatever. Some of the seeds removed at the end of the first year were filed and placed in soil, when they germinated healthily. In Chapter IX it is pointed out that some buoyant seeds of other Leguminous plants, such as Mucuna urens, would be apt to germinate abortively and to sink in crossing the more heated areas of tropical seas. The seeds of Cæsalpinia, judging from my experiments and observations noted on page 84, seem to be quite proof against such risks. This was well brought out in an experiment where seeds of the two species of Cæsalpinia were kept afloat for two and a half years in a vessel of sea-water together with seeds of Mucuna and Strongylodon. None of the Cæsalpinia seeds attempted to germinate in the sea-water; but with the other genera some of the seeds began to germinate, and sank in the course of the first warm season, when the water-temperature ranged from 75 to 90° Fahr.

The seeds develop their buoyancy during the great contraction

that, as before described, marks the final setting of the seed-coats and the ultimate maturation, as it is termed, of the seed. During this shrinking process the kernel also shrinks within the seed-tests, and cavities are thus produced within the seed-shell, on the relative size of which depends the buoyancy of the seed, neither the seed-shell nor the kernel possessing independent floating-power. These cavities, as illustrated in the figures given in Chapter XII, are of two kinds. That usually produced, being the one that mainly determines the buoyancy, is a large central hollow caused by the arching outwards of the cotyledons during the shrinking process, such as is found also in the seeds of Entada scandens, Mucuna urens, and some other Leguminous littoral plants. With such seeds the kernel never rattles when the seed is shaken, since the cotyledons lie in close contact with the seed-shell. The other kind of cavity is produced between the seed-shell and the kernel by the general or partial shrinking of the kernel away from the shell, the cotyledons remaining in apposition, as shown in the figures. When the shrinking away from the shell is general, the kernel lies loose within the shell, and the seed rattles when shaken. When the shrinking is partial the cavity is on one side of the seed and the kernel is fixed.

Professor Schimper (p. 164) remarks that the buoyant seeds of Cæsalpinia bonducella all rattle when shaken, and that it is to the incomplete filling of the seed-cavity, thus indicated by the loose kernels, that the buoyancy of the seed is due. The rattling of the kernel was, however, quite exceptional in the seeds handled by me, even in the case of originally buoyant seeds kept for five years. Seeds with loose kernels were, in fact, more frequent with non-buoyant seeds than with those that floated. Thus in Fiji I found that whilst with the buoyant seeds 17 to 20 per cent. had loose kernels, with non-buoyant seeds the proportion was as much as 60 per cent.

The normal cause of buoyancy is, therefore, a large inter-cotyledonary cavity with the cotyledons lying in close contact with the seed-shell; but the two kinds of cavity may sometimes be combined. Out of a number of buoyant seeds of Cæsalpinia bonducella examined by me, 80 per cent. owed their buoyancy solely to a large central cavity (4 to 5 mm. across). In 6 per cent. it was due solely to the shrinking of the kernel away from the seed-shell; whilst in 14 per cent. it was to be attributed partly to a reduced central cavity (2 to 3 mm. wide), and partly to a space outside the kernel. The only difference noted in the structure of the

buoyant seeds of C. bonduc was that the two kinds of cavities were more often combined.

The reason of the absence of floating power was clearly indicated in the non-buoyant Hawaiian seeds, where there was no central cavity, or it was represented by a narrow slit. The solitary buoyant seed found in the beach drift had a typical large central cavity. With the non-buoyant seeds of the inland species of the mountains of Vanua Levu it was ascertained that two-thirds had loose kernels with the cotyledons closely appressed. In the others there was a lateral cavity outside the kernel, the central cavity being only represented by a slit, a hair's width in breadth. In the non-buoyant seeds of C. bonduc, the central cavity was only 2 to 3 mm. wide, and the lateral cavities were small.

Respecting the influence of "station" in producing the differences in buoyancy, it cannot be said to be connected with the maturation of the seeds of inland plants under more humid conditions than those which prevail at the coast. In Fiji some of the littoral plants with buoyant seeds grow on the mangrove-trees in the shade and humidity of the swamps; whilst in Hawaii the inland plants of Cæsalpinia bonducella with their non-buoyant seeds thrive in exposed arid situations in districts of little rainfall, such as on scantily vegetated lava-flows. With non-buoyant seeds, where there is little or no cavity, the cotyledons are always thicker and moister than in the case of the seeds that float. Though associated with differences in station, as implied in the terms "coast" and "inland," the cause of the difference in buoyancy is not connected with different degrees of humidity, but with some other cause or causes acting on the spot which, while they favour the drying of the kernel in coast plants before the seed-coats finally set, impede it in the inland plants. That the seed does not subsequently acquire floating power, even after years of drying, was shown in several of my experiments.

The light, unopened prickly pods of both species float buoyantly, even when the inclosed seeds have no floating power. In an experiment on Cæsalpinia bonduc in Fiji the pods remained afloat after a month in sea-water. With those of C. bonducella in Hawaii I found that they floated for several weeks, and in one case a pod was afloat after three months. The pods dehisce on the plant; but they sometimes do not open sufficiently to allow the seeds to fall out. The pods, however, have to be torn off from the plant, and are not likely to occur in the drift. Indeed, they never came under my notice in any locality in the drift, and as an effective aid

to dispersal they must be disregarded. The buoyancy of the seeds and their well established distribution by currents render unnecessary an appeal to the floating pod.

The following is a summary of the foregoing remarks on Cæsalpinia bonducella and C. bonduc.

(1) The two species in Fiji are not always sharply distinguished, since intermediate forms occur, and here probably lies the explanation of the confusion that has sometimes occurred in diagnosing the species.

(2) Both are typical littoral plants, distributed over most of the tropical zone, and occurring in company in most of the Pacific archipelagoes; but they at times extend far inland.

(3) Though it is not unlikely that sea-birds may have aided in their dispersal, the oceanic currents have been the great agencies in their dispersal, as is indicated by the frequent transport of seeds in the Gulf Stream drift across the Atlantic, and by their occurrence in beach drift in various parts of the world.

(4) Having regard to the present arrangement of the currents and the distribution of the two species, reasons are given for the belief that their original birthplace was in the interior of the American continent.

(5) Notwithstanding the stony hardness of the seeds, when a notch is made in the outer skin a seed rapidly takes up water, and in a few days it becomes a soft and much swollen germinating mass. The author is inclined to think that this was the original condition of the seed, and that the rest-stage is an adaptation to secular differentiation of climate in later epochs.

(6) Unlike the seeds of other Leguminous littoral plants, those of Cæsalpinia are not likely to germinate abortively when floating in warm tropical seas, a risk that restricts the distribution of several littoral species.

(7) As tested by experiment, the seeds of both species are often able to float unharmed for years; but on the other hand seeds not infrequently have no floating power.

(8) Observation, however, shows that buoyancy goes with station, and that the general rule here applies that the seeds of coast plants float and those of inland plants sink.

(9) The nature of the influence of "station" on the seed-buoyancy is obscure; but it is evidently not connected with the usual differences between coast and inland localities, such as those concerned with exposure or shade, dryness of soil, relative humidity, and similar contrasts.

(10) The buoyancy of the seed is developed during the final shrinking process associated with its maturation, a large cavity between the cotyledons being usually produced.

Note.—Since most of the principal conclusions of this work are involved in my especial study of the littoral species of Afzelia, Cæsalpinia, and Entada, the reader is advised, if he wishes to form an opinion of the author's method of investigation, to read this chapter carefully through. With most other shore-plants, though in not a few cases studied with the same detail, the exigencies of space have often limited me to the employment of the general results in the appropriate chapters without entering into details. Should he desire to test any view of his own relating to plant-dispersal, he could not do better than begin with the materials here provided.

CHAPTER XVIII

THE ENIGMAS OF THE LEGUMINOSÆ OF THE PACIFIC ISLANDS

Leguminosæ predominate in tropical littoral floras.—The anomalies of their distribution in the Pacific islands.—They conform to no one rule of dispersal or of distribution.—Strangers to their stations.—The American home of most of the Leguminous littoral plants.—Summary.

IT is my intention here to gather up some of the "ends" of the great tangle presented by the Leguminosæ in the Pacific. When we look at the indigenous phanerogamic floras of Fiji, Samoa, Tahiti, and Hawaii we find that the Leguminosæ form 5 or 6 per cent. of the total in each of the three first-named groups, and only about 2·5 per cent. in Hawaii. The paucity of Leguminosæ in oceanic floras was long ago pointed out by Sir Joseph Hooker, whose work forms the foundation of much of our knowledge of insular plant-life. This is emphasised by Mr. Hemsley in his volume on the *Botany of the "Challenger" Expedition* (Introd. p. 25), where he makes the very significant remark that the Leguminosæ are wanting in a large number of oceanic islands where there is no truly littoral flora. The islands, however, here more especially referred to, are those of the southern Atlantic and Indian oceans, such as St. Helena, Tristan da Cunha, and Amsterdam. It is especially true of New Zealand, where the Leguminosæ barely make 2 per cent. of the total. Of the Polynesian islands, as he points out, it is not so correct; and, in fact, the proportion found in the Fijian, Samoan, and Tahitian floras, respectively, is much the same as that which characterises the British flora, namely, 5 to 6 per cent.

When we come to explain the paucity of the Leguminosæ in the Hawaiian flora we bring to light the singular principle that *Leguminosæ are far more characteristic of the littoral flora than of*

the inland flora of a Pacific island. About half of the Leguminosæ of Fiji and Tahiti are coast plants; and about 30 per cent. of the littoral plants of the islands of the tropical Pacific belong to this order. Since, therefore, Hawaii possesses much fewer shore-plants (30) than does Tahiti (55) or Fiji (80), the paucity of its Leguminous plants is readily accounted for.

We have next to notice a principle, which is, in fact, deducible from the first, namely, that *buoyant seeds are much more characteristic of the Pacific Leguminosæ than of any other order.* Three-fourths of the species have buoyant seeds, and, in fact, about a third of the littoral Polynesian plants with buoyant seeds or fruits belong to this order.

It may, therefore, be inferred that *the Leguminosæ owe their presence in the islands of the tropical Pacific mainly to the currents.*

From Mr. Hemsley's conclusion that the Leguminosæ are wanting in a large number of islands where there is no truly littoral flora, the presumptions arise that *when inland species exist that possess no capacity for dispersal by currents they are to be regarded as derivatives from the littoral flora, and that they owe their origin to a strand-plant possessing buoyant seeds originally brought by the currents.* It has been shown in the case of Afzelia bijuga and of Cæsalpinia that when Leguminous shore-plants extend inland the seeds often lose their buoyancy, and it is probable that divergence in other characters may occur, leading, as in the mountains of Fiji, to the development of a new species of Cæsalpinia. It is urged that by a continuation of the same process the inland species, Erythrina monosperma, has been developed in Tahiti and Hawaii, and the inland species, Canavalia galeata and Sophora chrysophylla, have been produced in the last-named group. All these species have non-buoyant seeds, and in all three cases there is no littoral species in Hawaii, it being assumed that the parent strand-plant has been driven inland from the beach. *It is not necessary that the littoral species should be now represented in the flora.*

It is remarkable that *in almost all cases the cause of buoyancy is of the non-adaptive or mechanical kind, due either to cavities formed by the shrinking of the seed-nucleus during the setting of the seed or to the light specific weight of the kernel.* There is but little to show that the buoyancy of the seeds of Leguminosæ is anything but an adventitious character of the seed, as far as its relation to dispersal by currents is concerned. Although this capacity has been the great factor in the wide distribution of the species, yet it

is evident that Nature here takes advantage of a quality that could never by its aid become a specific distinction. The upshot of the selecting process would be the dispersal by the currents of nearly empty seeds or seeds that have lost their germinating capacity.

The distribution of the Leguminosæ in the Pacific islands, and indeed of tropical islands generally, is often full of inconsistencies. This is the only order that sets at nought most of the principles established for the other plants of the sea-coast, and that defies the application of the laws of plant-dispersal now most in evidence. Take, for instance, the inexplicable affinity of Acacia koa, the well-known Koa tree of the Hawaiian forests, to Acacia heterophylla, a tree restricted to the Mascarene islands of Mauritius and Bourbon. Mr. Bentham, who placed them in the same group with three or four Australian species, even doubted whether the difference between the Hawaiian and Mascarene species amounted to specific rank. These two closely related Acacia trees of far-separated islands of the Indian and Pacific Oceans represent outliers of the great formation of phyllodineous Acacias that have their home in Australia (*Introd. Chall. Bot.* p. 26). As far as I can gather Acacia seeds have no known means of dispersal. Not even when the tree has a littoral station, as in the case of Acacia laurifolia in Fiji, have the seeds or pods any capacity worth speaking of for dispersal by currents. We must appeal to the birds ; but to what birds we may ask, unless it be to the extinct Columbæ and their kin, or to the Megapodes. Some of the other Hawaiian difficulties connected with the inland Leguminosæ are repeated in the Mascarene Islands. Thus, Bourbon, like Hawaii, has its inland species of Sophora of the section Edwardsia.

In their irregular distribution the Leguminosæ of the Pacific islands are often a source of perplexity to the student of plant-dispersal. Take, for example, the inland Erythrina, E. monosperma, of Hawaii, Tahiti, and perhaps New Caledonia. Then look at the singular distribution of the Sophoras of the Edwardsia section in Chile and Peru, Hawaii, New Zealand, Further India, and Bourbon. The botanist, again, finds a climber like Strongylodon in the forests of Fiji, Tahiti, and Hawaii, and he picks up the seeds on the beaches of those islands and notices that they float unharmed for many months in the sea, yet when he pays heed to the distribution of the genus he finds that it only comprises four or five species, and that it occurs outside the Pacific only in the Philippines, Ceylon, and Madagascar. The extraordinary distribution of Entada scandens in the Pacific islands has been before

alluded to in these pages. Here we have a plant, the seeds of which are known to be transported unharmed by currents all round the tropics. Yet it is absent from Hawaii and from almost all of the islands of Eastern Polynesia. In many cases an endeavour has been made in this work to explain these difficulties. But the order in the Pacific teems with such difficulties. We may ask with astonishment why it is that the genera, and sometimes even the separate species, of the Leguminosæ seem so often to follow in each case a principle of their own.

Plants of this order in the Pacific conform to no one rule of dispersal or distribution, whether we regard a species, a genus, or the whole order. Take, for instance, the presence in Hawaii of Canavalia galeata, a plant that, as we know it now, could not possibly have reached there through the agency of the currents, and the absence from the same group of Entada scandens that could have been readily transported there by the currents from America. Or, if we take the whole order and look at the structures connected with the buoyancy of the seeds, we find two types of structure and the elements of a third. Then, again, whilst most littoral plants with buoyant seeds retain the buoyancy of their seeds when they extend inland, Leguminous shore-plants, like Afzelia bijuga and Cæsalpinia bonducella, when they extend inland in Fiji and Hawaii, lose in great part or entirely the floating power of their seeds.

Furthermore, most strand-plants, being typically xerophilous in character, when they extend inland shun the forests and prefer the dry soil and sparsely vegetated surface of the open plain ; but the Leguminous genera and species (Mucuna, Afzelia, Entada, &c.) when they leave the coast take to the forests, growing usually as stout lianes, but sometimes as tall trees. Here again the Leguminosæ seem to follow a principle of their own. As far as I know, this is the only order in the Pacific possessing forest-trees which, as in the case of Afzelia bijuga in Fiji, are equally at home in the woods of the interior and of the coast.

Indeed, judging from Professor Schimper's observations, the littoral Leguminosæ of the tropics often display a physiological constitution that seems in some respects out of touch with their surroundings. They may, as in Sophora tomentosa and in Canavalia, present the xerophytic character of strand-plants, but frequently they are not halophilous or "salt-loving," like other plants associated with them on the same shore-station. They are often shy of salt in their tissues, though able to thrive in salt-rich localities. That capacity which strand-plants usually possess of storing

up chlorides in their tissues, and especially in their leaves, without injury to themselves, is but slightly possessed by such characteristic shore-plants as Canavalia, Pongamia glabra, and Sophora tomentosa. This capacity, which, as Professor Schimper indicates, goes to determine whether or not plants are capable of living in salt-rich localities, has often no determining influence with the Leguminosæ. (See Note 60.)

Though the plants of this order form such a large element in the strand-flora of the Pacific islands and of the tropics generally, they seem in other respects, besides those just referred to, to act as if they were strangers to the station. Look, for instance, at the readiness of the floating beans of Mucuna, Strongylodon, &c., to germinate, as shown in Chapter IX, in the tepid waters of the warmer areas of the tropical oceans. This is a great deal more than a disturbing factor of distribution. It is significant also of the plants being out of touch with their dispersing agencies.

One may notice in conclusion the fact brought out in Chapter VIII that nearly all the littoral plants dispersed by the currents that are common to the Old and the New Worlds belong to the Leguminosæ. This is held to indicate that their home is in America, since that continent distributes but does not receive tropical littoral plants dispersed by currents.

Summary.

The Leguminosæ are far more characteristic of the littoral flora than of the inland flora of the Pacific islands ; and since the greater number of them have buoyant seeds, it follows that this order mainly owes its presence in this region to the currents.

As it has been shown that in a large number of islands where there is no littoral flora the Leguminosæ are wanting, the presumption arises that when, as in Hawaii, inland species occur which at present have no capacity for dispersal by currents, they have been derived from strand-plants originally brought by the currents, even though such shore species no longer belong to the flora.

As far as its relation to dispersal by currents is concerned, the buoyancy of the seeds of Leguminosæ is merely an adventitious character, and the structure connected with it has no specific value.

Plants of this order in the Pacific are a source of much perplexity and conform to no one rule of dispersal, whether as regards their disconnected distribution, their means of dispersal, the

structural cause of buoyancy, the loss of buoyancy of inland species, and in other particulars. Even in their physiological constitution they are often at variance with the bulk of littoral plants when they grow on the sea-shore, since typical beach-plants of the order, though thriving in salt-rich localities, are shy of salt in their tissues.

It is probable that whilst the Pacific islands have derived most of their littoral plants that are dispersed by currents from the tropics of the Old World, they have received most of their strand Leguminosæ from America.

CHAPTER XIX

THE INLAND PLANTS OF THE PACIFIC ISLANDS

Preliminary Comparison of the Physical Conditions of Hawaii, Fiji, and Tahiti

Introductory remarks.—The trànquil working of the winds and currents contrasted with the revolutionary influence of the bird.—The Hawaiian, Fijian, and Tahitian groups.—Their surface-areas and elevations.—Their climates. —The mountain climate of Hawaii.—The rainfall of the three groups.— Summary.

Introductory Remarks.

I WILL carry my readers back to that moment when we began to investigate together the composition of the floras of the islands of the tropical Pacific from the standpoint of dispersal. It will be remembered that after collecting all the fruits and seeds of a particular island we placed them in sea-water, and that some nine-tenths of them went to the bottom at once or in a few days. We found, speaking generally, that the buoyant seeds and fruits belonged to coast plants, whilst those at the bottom of the vessel proved to be obtained from inland plants. Since that period we have been occupied in following up the clue supplied by the floating seeds and fruits. In their company we have travelled far beyond the Pacific islands. We have not only seen their fellows in other parts of the tropics, both on the coral atoll and on the continental coast, but we have met their representatives on the beaches of Europe and of temperate South America. We have followed them in their ocean traverses round most of the tropical zone, and on the way we have naturally interested ourselves in the question of the currents. We have weighed these seeds and fruits and have compared their specific weight with that of sea-water. We have

cut them up and carefully examined them, and under their guidance we have explored the mangrove-swamps both of Polynesia and of Ecuador, and have penetrated the mysterious *cul de sac* of vivipary. Having formed our opinion of them, we now bid the subject farewell, and stand once more on the same Pacific beach where, it seems so long ago, our investigations began.

For the seed and fruits lying at the bottom of the sea-water we have to appeal to other agencies than to that of the currents if we wish to inquire into their means of arriving at this island. In imagination we leave the reef-lined shores for the interior, and exchange the exhilarating surroundings of a coral beach, where "the sky is always blue and the wind is always true," for the arid conditions of an inland plain, or for the humid conditions of the forest, where the rain is incessant and the cloud-cap and mist seemingly eternal. When we look at the motley collection of fruits and seeds obtained in such localities, we are at a loss to know where to take up the clue. After vainly endeavouring to obtain some inspiration as to the manner of commencing the inquiry, we do what all good naturalists in the Pacific islands do from force of habit when they meet with difficulties of any kind—we sit down and light our pipes. Then come a flood of old memories and old trains of thought that came to us years before on some mountain-top or in a shady gorge or on some river-bank, in regions Pacific and non-Pacific, and by degrees our ideas shape themselves and we begin to think the matter over in an orderly fashion.

When the winds first brought the spores of ferns to this Pacific island, the ocean currents brought the seeds and fruits of littoral plants, and the birds transported the seeds and "stones" of various inland species. All three agencies have been working side by side since the earliest stage in its history. Yet it is only in the work of the wind and the current that we find any indication of stability in the floral history of the island. With the work of the bird it has been very different. Since the first bird carried seeds to this locality all else has been turmoil and change. Wave after wave of migrant plants has overrun the interior of the island, and all have left their mark; but the great distributing factor and disturbing agent has always been the bird. Genera have been born and have disappeared, and in their place new genera have arisen. Whole families even have participated in the revolutions of the plant-world, and species have grown rankly in the great confusion. Last of all came man with his cultivated plants and his weeds, introducing new elements of change and discord into the island, and often up-

setting the floral economy altogether. The history of man's most troubled epoch would not be more full of catastrophes and great events than the history of the plants of this Pacific island. Yet through all these changes the winds and currents have been quietly carrying on their work, bringing the same plants to beach and hill-side that they did before the age of unrest began.

The monotonous character of an island flora that has been supplied by the winds and currents can be readily imagined. For their variety the floras of the Pacific islands are mainly indebted to the bird, the great disturber of the peace of the plant world. We cannot attach too much importance to the contrast in the results produced by these several agencies in stocking a Pacific island with its plants. On the one hand we have the tranquil working through the ages of the winds and currents. On the other hand there has been the revolutionary influence of the bird. One cannot doubt that many of the species of flowering plants now growing on the beach and many of the ferns on the upper mountain-slopes have witnessed changes within the forest-zone of the island, such as an antediluvian might record if he had lived through the ages to the present time.

Now, what are these changes? How has the bird acted unconsciously such a determining part? These are questions which I will endeavour in some way to answer as one picks one's path slowly through the various epochs in the plant-history of these islands. We already are fairly well acquainted with the beginnings of a flora either on a coral atoll or on an ordinary tropical beach. What we have yet to learn is the subsequent history of the flora. When Dr. Treub undertook, in 1886, his now celebrated examination of the new flora of Krakatoa after the great eruption, he commenced a series of observations which will no doubt be prolonged into future centuries. Botanists a hundred and two hundred years hence will complete a long chain of observations which will be unique as a record of plant-colonisation; and science is deeply indebted to Prof. Penzig for making, in 1897, the second examination of the new flora. Though deprived of the valuable record that future generations will possess for Krakatoa, we yet have at our disposal in the completed process displayed by many a Pacific island a means of working backward and in a sense completing the history.

In order to attack this problem I have mainly confined myself to the Fijian, Tahitian, and Hawaiian floras, taking the three archipelagoes just named as the centres of the regions in which they

occur. These three groups lie near the three angles of the triangular area of the Pacific over which the various archipelagoes are scattered. They are thus geographically well placed for an inquiry into the subject of plant-dispersal over this ocean, and each of their floras has been investigated by botanists of various nationalities—American, Austrian, British, French, German, and Italian. The Fijian area may be regarded as including the adjacent Samoan and Tongan groups, though the individual group or the whole area will always be in this work particularised. In the same way Tahiti will be viewed as usually representative of the larger islands of the surrounding groups of the Cook and Austral Islands and of the Marquesas; and under the designation of the Tahitian area or Tahitian region there will be generally included the Paumotu archipelago.

Comparison of the Areas and Altitudes of Hawaii, Fiji, and Tahiti.

Since differences in physical conditions have played an important part in plant distribution in these groups—such, for instance, as in determining the development of a mountain flora or in favouring the relative abundance of particular types of plants—it is at first essential to obtain a general idea, in the case of the larger islands of each group, of their size and elevation, and of the more conspicuous differences in their climates.

Hawaii, the largest island of the Hawaiian archipelago, has an area of 4,210 square miles. All the other islands of the group are considerably smaller—Maui, the second in size, having a surface of 760 square miles; Oahu coming next; and after it Kauai, with an area of 590 square miles. The area of Viti Levu, the largest island of the Fijis, is 4,112 square miles, being thus closely similar to that of the island of Hawaii; Vanua Levu, the second in size, is 2,433 square miles in extent; whilst the other important islands of the group are much smaller, Taviuni, the third in size, having an area of 218, and Kandavu an area of 125 square miles. Tahiti, the largest and loftiest island of Eastern Polynesia, has a surface of about 400 square miles; whilst most of the other elevated islands of the groups around are considerably smaller.

In respect of elevation above the sea, there is a great contrast between the islands of these three regions. Taking the Hawaiian Group first, we notice that the three principal mountains of the large island of Hawaii rise in the cases of Mauna Kea and Mauna

Loa to between 13,000 and 14,000 feet, and in that of Hualalai to rather over 8,000 feet. Situated between these three mountains there is an extensive tableland or plateau, known as the Cattle Plains, which is elevated between 4,000 and 6,000 feet, and has an area of not less than 200 square miles. At least a third of the whole area of the island exceeds 4,000 feet in altitude. In the eastern portion of Maui the huge mass of Haleakala rises to rather over 10,000 feet; whilst Mount Eeka, in West Maui, rises in bulk to some 6,000 feet. The island of Kauai, which is elevated between 5,000 and 6,000 feet, possesses in its interior an elevated tableland 40 square miles in extent and 4,000 feet in altitude. Oahu attains in Mount Kaala a maximum elevation of 4,000 feet, but 3,000 feet is the limit of the other peaks, and much of the island is low in elevation.

On the other hand, in the two largest islands of Fiji, namely, Viti Levu and Vanua Levu, we find in the first-named only two or three of the highest mountain peaks rising to between 4,000 and 5,000 feet; whilst the highest peak of Vanua Levu reaches only to about 3,500 feet. Amongst the lesser islands, Taviuni just reaches the level of 4,000 feet, and Kandavu, the next in height, about 2,750 feet. The area of the land-surface in this group that is above a level of 4,000 feet is very scanty, and for the botanist a negligible quantity, so that for purposes of comparison the Fijian Islands, as far as elevation is concerned, correspond to the lower levels of the Hawaiian Islands, that is, to the areas below 4,000 feet. The same may be said of the Samoan Islands with the exception of a limited area in the centre of Savaii, where a peak rises to 5,400 feet above the sea.

Coming to the Tahitian region, we find that Tahiti, the most elevated island, attains an extreme height of about 7,300 feet; but from its surface-configuration it is evident that not one-tenth of the area exceeds 5,000 feet; yet since its total extent is about 400 square miles there must be an elevated region of some 30 square miles in amount comparable in some degree with the uplands of Hawaii. The Marquesas, next in order in size and height, attain a maximum elevation of about 4,000 feet; whilst, amongst the Cook and Austral Groups, Rarotonga reaches a height, according to Mr. Cheeseman, of 2,250 feet. Excepting the limited elevated area of the uplands of Tahiti, there is nothing in Eastern Polynesia corresponding to the higher levels of the Hawaiian Islands over 4,000 feet. We formed the same conclusion for Fiji, and I may add that it applies to the whole area of Fiji, Samoa, and Tonga,

since the solitary peak of Savaii in the second-named group, which reaches 5,400 feet, alone represents a high-level area. The uplands of Hawaii—that is to say, the elevated region between 4,000 or 5,000 feet and 14,000 feet (strictly speaking 13,800 feet)—are therefore almost unrepresented amongst the oceanic groups of the South Pacific; and it is only in the peak of Savaii and in the limited high levels of Tahiti that we would expect to find their conditions reproduced. The great effect that this contrast implies in determining differences between the floras of the Hawaiian, Fijian, and Tahitian regions will become apparent as we proceed in this discussion.

Comparison of the Climates of Hawaii, Fiji, and Tahiti.

Before comparing the climatic conditions in the three groups, it may first be remarked that since they lie, roughly speaking, at not very dissimilar distances north and south of the equator a great contrast is not to be expected in so far as they agree in elevation. The mean latitudes do not differ greatly, that of Hawaii being 20° to 21° N., and those of Fiji and Tahiti both about 18° S. The climate of both groups is tempered by the north-east trade in the one region and by the south-east trade in the other. Still there is a difference in the temperature and dryness of the air which noticeably distinguishes Hawaii from Fiji, and to a less extent from Tahiti. The mean temperature of the Hawaiian Islands would be 74° or 75°; whilst that of Tahiti is placed at 76° to 77°, and that of Fiji at 79°. But it is to be observed that to a person residing in Fiji after a residence in Hawaii the climate is perceptibly warmer, more humid, and more enervating. No doubt this is in part connected with the greater dryness of the air in Hawaii, where the average relative humidity at Honolulu is placed at 72 per cent., and it must be much less on the Kona coast on the dry side of the largest island. It is, however, probable that the Hawaiian climate was less dry before the destruction of the forests, and that the contrast with the Fijian climate was then less pronounced.

The great distinguishing feature, however, of the Hawaiian Islands is to be found in their mountain climate. This is not represented in Fiji, but slightly in Samoa, and to a small extent in Tahiti; and I will now refer more particularly to this important subject.

In the uplands of the large island of Hawaii, on the tops of the

lofty mountains 10,000 to 14,000 feet above the sea, we have a mean temperature only found far north. Snow lies often on these barren summits in winter, more particularly on Mauna Kea, which thus derives its native name of the White Mountain. The details of my meteorological observations on Mauna Loa will be found in Note 61; and only some of the general results will be referred to here.

The mean temperature for the period of twenty-three days passed by me on the summit of Mauna Loa (13,600 feet) between August 9th and 31st, 1897, was 38·5° F. The mean temperature for a period of twenty days from December 24th, 1840, to January 12th, 1841, during which Commodore Wilkes and his party were making pendulum observations on the summit of the same mountain, was approximately 33·5° (see Note 61). From these results, which are tabulated below, it will be seen that the mean annual temperature would be probably about 36°, which is scarcely comparable with any continental climate, since only a difference of a few degrees is indicated between the mean temperatures of August and of a similar period in mid-winter. I may add that although it was in the summer month of August, water froze inside my tent during twenty out of the twenty-three nights passed on the top. We may, therefore, infer that the temperature falls below the freezing point at night practically throughout the year. It will be seen from the table that the mean annual temperature for the summit of Mauna Loa, as here computed from the observations of Commodore Wilkes and myself, comes very near to that which might be estimated by employing Hann's tables of variation in temperature with altitude on tropical mountains (see Schimper's *Plant-Geography*, iv. 691).

WINTER AND SUMMER TEMPERATURES ON THE SUMMIT OF MAUNA LOA (13,600 FEET), IN DEGREES FAHRENHEIT.

Observer.	Period.	Mean daily range.	Lowest.	Highest.	Mean for period.	Approximate yearly mean.
Wilkes...	Dec. 24, 1840—Jan. 12, 1841	17° – 50° = 33°	13°	55° ?	33·5°	36°
Guppy ...	Aug. 9—31, 1897	23·2 – 53·8 = 30·6	15	61·2	38·5	

Estimated mean annual temperature of the summit of Mauna Loa, taking that of the coast at 75°, would be 34° if the rate of increase was the same as on Mount Pangerango in Java (1° per 328 feet).

The great daily range of temperature is one of the most striking features of the climate of the summit of Mauna Loa. The extreme recorded by me was 38·7°, whilst Wilkes registered as much as 42°. As on most lofty mountains the dryness of the air, as indicated by the relative humidity, was usually great. The average percentage during my stay between 8 and 9 A.M. was 44, at midday 43, and between 5 and 6 P.M. 56. This may be contrasted with 72, the average for the year at Honolulu. In the tropics the mean for the year in the lower levels often rises to 80 and over; and it can scarcely be doubted that the Hawaiian climate is generally drier than it was before the destruction of the forests. The lowest relative humidity recorded by me on the summit of Mauna Loa was 20 per cent. Junghuhn on the summits of two mountains in Java, 10,500 and 11,500 feet in height, recorded percentages as low as 5 and 13. Further details relating to this subject are given in Note 61. The rainfall on the top of Mauna Loa is probably very slight. During my sojourn rain was noted on six days, but on only two could it be measured, and the total fall could not have amounted to over a third of an inch.

The mean annual temperature of the great forest-zone at the elevations where it displays the greatest luxuriance of growth on the island of Hawaii, that is, between 4,000 and 6,000 feet, would be estimated at 63° and 57° F., if we take the rate of decrease before employed of about three degrees per 1,000 feet. But remembering the heavy rainfall in this region and the usual occurrence of a protecting belt of cloud during the day, this might seem to be too high. According, however, to a table given by Mr. Jared G. Smith in his annual report of the Hawaii Agricultural Experiment Station for 1902, the average temperature at 4,000 feet would be 65°. I cannot help thinking this is excessive as an average for the island. In the latter part of May, 1897, the mean temperature during my sojourn of twelve days at elevations between 6,000 and 6,700 feet around the slopes of Mauna Kea was 51·2°; whilst for eight days in the first part of June in the same region the mean temperature was 58·2° at an altitude of 4,000 to 4,300 feet.

It is possible, as I have pointed out on a later page, to recognise in the different zones of vegetation the floras of a variety of latitudes; and these zones are to a large extent controlled by temperature as well as by other conditions. Thus the Fijian would be amongst familiar vegetation on the lower slopes of Mauna Kea, whilst the Maori would be at home halfway up the mountain-

slopes, and the African from the upper forests of Kilima Njaro and Ruwenzori would find in the higher levels much to remind him of his native land.

The upper woods extend usually to 8,000 or 9,000 feet above the sea, and vegetation of a scrubby character occurs as high generally as 10,000 or 11,000 feet. The highest regions present only a barren rocky waste.

THE RAINFALL.

The Hawaiian Islands.—Although on account of the extensive deforesting of the Hawaiian Islands since their discovery the contrast between this group and that of Fiji is now, as regards rainfall, somewhat emphasised, it is almost certain that in early times the contrast was much less marked. In the lower levels the natives and sandalwood traders in the past, and the agriculturists in the present, have accomplished much in this direction. Between 1,000 and 3,000 feet, whole forests were in my time disappearing under fire and axe for the coffee plantations. Above those levels up to the higher limits of the woods, cattle were destroying the forests in a wholesale fashion ; whilst foreign insects were proving themselves almost as great enemies to the vegetation. I remember an enterprising agriculturist explaining to me how he cleared the land of forest around his station. A large tract having been fenced in, the cattle were introduced. After destroying the undergrowth and the young trees, the animals attacked the bark of the trees, and in a year or two, without fire or axe, the land was cleared. The consequence of this unchecked destruction of the forests was in my time becoming only too evident. When I passed through Ookala, on the Hamakua coast, at the end of May, 1897, there was a water famine. Water was sold at a quarter of a dollar a bucket, and the allowance for a family was three oil-cans a week. Stealing water was a crime and punished by the plantation authorities by dismissal or a five-dollar fine.

If we could look back for fifty or sixty years—I am now quoting from the reports of Prof. Koebele and Dr. Stubbs—we should see large forests where we now see barren slopes and plains. Originally forests covered the upland plateaux and mountain slopes of all the islands. Now much of the original forests has been removed, and large areas of naked soils and bare rocks remain. The present forest area, writes Mr. Giffard, the editor of the *Hawaiian Forester* (August, 1904), is about 20 per cent. of

the islands, a small fraction of what it was a hundred years ago. It is, however, very satisfactory to learn that American energy is now combating this evil. Already in the January number of the same journal is to be found a report by Mr. W. L. Hall, of the Bureau of Forestry, on "The Forests of Hawaii"; and now, under the charge of Mr. Jared G. Smith, institutions have been formed and experiment stations have been established for "the intelligent and skilful cultivation of the soil." Hawaii owes much to the United States Department of Agriculture. May we in England take the cue in the case of our own Crown colonies!

Under these circumstances the comparison of the present rainfall of Hawaii must be carried out with discrimination. But it may be at once observed that to make a contrast in detail between the rainfalls of these three groups is quite beyond the province of this work; and this remark applies also to the other observations on the climatic conditions. I can only treat the subject in an illustrative fashion in connection with the general subject of their floras.

Thanks to Professor Lyons, the Government meteorologist, the rainfall has long been systematically investigated. It may be said to range anywhere between 10 and 300 inches. As in most groups within the trade-wind belts, there is a great contrast in the rainfall between the weather and leeward sides of the islands, which is well exhibited in the large island of Hawaii. Whilst in the Hilo district on the wet side of the island the annual rainfall near the coast is about 120 inches, on the Kona coast of the dry side of the island it may be anything between 20 and 50 inches and it may fall to less than 10. The effect of elevation is, however, evident on both the weather and lee sides of the island. Thus at a height of 1,650 feet in the Hilo district it is as much as 180 inches, and at a greater elevation 210 inches. At a height of about 1,600 feet at Kealakekua, on the dry side of the island the average yearly rainfall, according to the results kindly supplied to me by the Rev. S. H. Davis, was for the six years, 1891–6, 60 inches. On the beach, as he says, it is "very much less," probably not 30 inches. Dr. Maxwell, in his report on "Irrigation in Hawaii," mentions a locality in Maui where the rainfall at the sea-shore was 28 inches, and at a height of 2,800 feet up the mountain side as much as 179 inches. In the region of the cloud-belt, which coincides with that of the forest-zone on the slopes of the great mountains of Hawaii and extends up from about 3,000 to 7,000 or 8,000 feet above the sea, the average annual rainfall would probably be rarely under 200 inches, and in some localities it might approach 300 inches. There

are some particularly wet mountains, and amongst these may be placed the high table-land of Kauai (4,000 feet) and the flat summit of Mount Eeka (6,000 feet) in West Maui. Here in a region almost of eternal mist we have developed a special bog-flora.

Hillebrand describes the flat top of Mount Eeka as "wrapt in a cloud of mist nearly the whole year." Whilst descending this mountain I was overtaken by the darkness at a little under 5,000 feet above the sea. Through the night there was a continuous soft rain, or rather a heavy wet mist, and I passed it under conditions suggestive of living in a sponge. Everything was reeking with moisture. The air was saturated with it, and water dripped from every leaf and branch, whilst the ground on which I stood was soft and yielding and soaked with water like a sponge. The surface was cut up by numerous narrow water-channels ten to twenty feet deep and only a couple of feet wide, their very existence almost concealed by ferns, whilst torrents rushed along at the bottom and kept up a strange music through the night. This was the longest night I have ever experienced, as my standing-ground was very limited, and with a water-channel a foot or two away on either side I had to keep on my legs until the dawn.

Above the cloud-belt, at elevations of 10,000 feet and over, the rainfall is evidently very small. I have before remarked that during my stay of twenty-three days (August 9–31) on the summit of Mauna Loa (13,600 feet) the rain did not exceed one-third of an inch in amount. I have by my side the report to the Weather Bureau, compiled by Prof. Lyons, on the rainfall of this large island of Hawaii for the entire month (August, 1897); and it enables one to make a comparison, in some respects unique, of the distribution of the August rainfall on Mauna Loa, from its base to its summit, where it occupies the breadth of the island. Whilst on the east or wet side from the coast up to 1,500 feet amounts ranging from 11 to 15 inches were measured, on the west or dry side between one and two inches were registered at the coast, and 10 inches at Kealakekua, about 1,600 feet above the sea. But the level of maximum precipitation would lie much further up the mountain slopes on either side, probably at an altitude of 4,000 or 5,000 feet, and here the rainfall for the month could not have been less in either case than 20 inches. Above this line of greatest rainfall the amount of atmospheric precipitation would become less and less until beyond the upper forest zone above 10,000 feet to the summit (13,600 feet) the quantity would be very small; and

judging from my observations, that covered three-fourths of the month, the rainfall on the top of the mountain for August would not have far exceeded half an inch.

The dry climate of the summits of Mauna Kea and Mauna Loa is reproduced on the tops of the Java mountains and on the summits of the Owen Stanley Range in New Guinea. Sir W. Macgregor found a fine and dry climate on the top of the mountains last named, beyond the limits of the forests, which extend to 12,000 feet above the sea. Below lay the cloud belt, a zone of moss and fog, where at an elevation of 7,000 to 8,000 feet everything was reeking with moisture (*Journ. Roy. Geogr. Soc.* 1890). Observers at the coast often little imagine, when looking at a cloud-concealed mountain peak, that although the cloud-belt from below looks black and lowering and rain is falling heavily in the gloomy forests, there is on the upper side a region of bright sunshine, and that the peak stands out, unseen by them, above a sea of clouds sparkling brilliantly in the sun and dazzling in their whiteness. It will be seen from the table given in Note 61, that during my sojourn on the summit of Mauna Loa the sky was cloudless or almost free from cloud during nearly half the time. The mean cloudiness in the forenoon for twenty-two days was 1·3 and for the afternoon 3·5, whilst the nights were cloudless.

The Rainfall of Fiji.—The rainfall of Fiji is known to be very large. In illustration I will take Vanua Levu, the second largest island, partly because of my familiar acquaintance with it, and partly because I have at my disposal measurements for both the lee and weather sides of the island—the first dry and characterised by a scanty and peculiar vegetation, the second humid and densely forested. At Davutu, near the sea-level on the weather or wet side of the island, the average yearly fall for a period of sixteen years up to 1898 was 160 inches (these observations were made in the grounds of the manager's house and I am indebted to Mr. Barratt for allowing me to inspect them). The mountainous backbone of the island, which has an elevation ranging usually from 2,000 to 3,000 feet, is generally in the rain-clouds. During the months I was occupied in examining the geology of these mountains, it was a common experience to be drenched to the skin all day long, and I cannot doubt that the annual rainfall in the higher levels must often reach 300 inches. Those familiar with the "sunburnt" lands or "talasinga" plains that mainly form the north or lee side of the island, would expect a great difference in rainfall as compared with the south or weather side. There is a marked

difference, it is true, but it is far less than we might have looked for. At Delanasau on the north coast, less than a hundred feet above the sea, the mean rainfall for seven years (1871–77), according to the observations of Mr Holmes, was 113 inches, and the range 80 to 159 inches (see Horne's *Year in Fiji*). In discussing the origin of the arid-looking plains on the north or lee side of the island in Note 22, I have shown that the explanation is to be found not so much in the rainfall as in the dryness of the air as indicated by the relative humidity.

The rainfall varies greatly in and around Vanua Levu, but there is little doubt that by far the greatest bulk of the rain is precipitated on the upper weather slopes of the mountainous backbone of the island. Taviuni, which lies off its weather coast, is probably the wettest among the smaller islands of the group. In 1877, when 80 inches were recorded by Mr. Holmes at Delanasau on the north side of Vanua Levu and 73 inches at Levuka in the island of Ovalau, 251 inches were measured in Taviuni at Ngara Walu 564 feet above the sea; and in 1875 the rainfall recorded at Taviuni was 212 inches, and at Delanasau 126 inches (Horne).

Fortunately, the Fijian islands have not been long enough occupied by the whites to produce much effect on the rainfall through the destruction of the forests. A significant warning, however, has been given in the vicinity of Levuka. The woods of the hills around the town, as we learn from Mr. Horne, were cut down to prevent them from affording shelter to the unfriendly natives of the interior, the result being to reduce the number of rainy days in a few years from 256 to 149 per annum.

The Tahitian rainfall.—The annual rainfall of the coast districts of Tahiti is placed at about 50 inches (*Encycl. Brit.* vol. 23); but, as is observed by Nadeaud and Drake del Castillo, the rain-clouds gather round the peaks, and the precipitation is much greater in the interior than at the "littoral," with a corresponding result in a striking difference between the vegetation of the two regions. Probably, therefore, the rainfall for the year on the wooded mountain slopes and at the heads of valleys where the vegetation is most luxuriant would be over 100, and perhaps as much as 150 inches in places. (The annual rainfall in Rarotonga is, according to Cheeseman, about 90 inches.)

It is evident that in the three groups of Hawaii, Fiji, and Tahiti, the rainfall varies greatly with situation and with elevation; but the contrast is much greater in Hawaii than in Fiji. Thus there would be scarcely any place on the lee side of Vanua Levu where

the average annual fall would be less than 80 or 90 inches, except perhaps in the Undu Promontory, whilst on the lava-bound coast of the west or lee side of Hawaii, it may be reduced to 20 inches and less. There is no doubt that this was to some extent the case in pre-European times, since Fiji must have possessed for ages, on the northern sides of the larger islands, its arid "talasinga" or "sun-burnt" plains; and in the island of Hawaii there must have always been vast, scantily vegetated lava fields at the sea-border. It is probable, however, that it is in the older islands of the Hawaiian group, those where the volcanic forces have been long extinct, that the rainfall has been chiefly affected by deforestation. Speaking generally, in pre-European times the climatic conditions of the lower levels of the group, that is below 4,000 feet, which are alone comparable with Fiji, were less contrasted with the climatic conditions of the Fijian islands than they are at present. By reason of their great elevation, the Hawaiian islands present a mountain climate not found in Fiji, and scantily represented in Tahiti. It is, therefore, in the flora of the Hawaiian uplands that we should expect to find the great distinguishing feature between that group and Fiji.

Summary of the Chapter.

(1) Whilst the winds and the currents have been working tranquilly through the ages, bringing always the same vascular cryptogams and shore-plants to the Pacific islands, the bird has ever been a disturbing factor in the inland flora, and changes often of a revolutionary character have taken place from time to time within the forest-zone.

(2) In the discussion of the inland plants of these islands, the Fijian, Tahitian and Hawaiian areas are taken as centres of development and dispersal, and as including the groups around.

(3) On account of the contrast in physical conditions presented by these archipelagoes, differences with which some of the most distinctive features of the floras are to be connected, a comparison of the islands from this standpoint is first necessary.

(4) Since the largest islands of the Fijian and Hawaiian areas are from five to ten times the size of Tahiti, the largest island of the Tahitian region, we would expect to find in the two first-named groups a much more varied flora.

(5) There are three huge mountain-masses in the Hawaiian group which rise to between 10,000 and 14,000 feet, and there is in

the aggregate a large area elevated more than 4,000 feet above the sea. These elevated regions are almost unrepresented in the southern groups, the Fijian islands being only comparable with the lower levels of the Hawaiian islands below 4,000 feet, and the same is true of all the groups with the exception of a limited area in Tahiti, where the mountains reach a height of 7,300 feet, and of the solitary peak of Savaii in Samoa, which attains an altitude of 5,400 feet. Thus the conditions for a high-level or mountain flora which exist in Hawaii are not to be found in Fiji, but slightly in Samoa, and to a limited extent in Tahiti.

(6) From their position with regard to the equator and with reference to the trade-winds a great contrast between the climates of these three regions—the Fijian, the Tahitian, and the Hawaiian—is, as far as the islands agree in elevation, not to be expected, and in fact does not exist. The Fijian climate, however, is now warmer and more humid, and the general rainfall is greater than in the case of Hawaii, but it is probable that these differences were much less pronounced before the destruction of the Hawaiian forests, which has been in progress since the discovery of the group.

(7) Anywhere around the coasts of the larger Fijian islands we might expect an annual rainfall of not less than 80 or 100 inches. In the Hawaiian group the rainfall at the coast may be anything between 10 and 100 inches, but is generally less than 50 inches. In Tahiti, at the coast, it is 50 inches. In all cases the rainfall increases greatly with elevation. In the Fijian mountains the rainfall probably varies between 200 and 300 inches. In the Hawaiian forest-zone it would range probably between 100 and 200 inches, though this is probably exceeded in a few localities. In the Tahitian uplands it would doubtless exceed 100 inches and approach 150 inches.

(8) Quite a different climate prevails on the lofty summits of Hawaii 13,000 to 14,000 feet above the sea. Here the snow lies in winter, and the mean annual temperature is only a few degrees above the freezing point, probably about 36° F. The difference between the mean summer and winter temperatures is very small, and does not exceed five or six degrees. Water freezes here during nearly every night of the year. The daily variation of temperature is very large, the average being probably about thirty degrees. Great dryness of the air prevails, the average relative humidity in August, 1897, being about 43 per cent. There is but little rain. The sun shines fiercely, and the sky is usually clear.

(9) All Pacific climates are represented in the Hawaiian mountains, that of Fiji on the lower slopes, that of New Zealand half way up, and that of the Antarctic islands on the summits.

(10) When contrasting the floras of Fiji, Tahiti, and Hawaii, it will be necessary to restrict our comparison in the case of Hawaii to the lower slopes below 4,000 or 5,000 feet; and we should expect the Hawaiian mountain flora to be scantily represented in Tahiti, and scarcely at all in Fiji and Samoa.

CHAPTER XX

THE EPOCHS IN THE FLORAL HISTORY OF THE PACIFIC ISLANDS

The Age of Ferns

The epochs in the plant-stocking.—The age of ferns and lycopods.—The relative proportion of vascular cryptogams in Hawaii, Fiji, and Tahiti.—The large number of peculiar species in Hawaii.—The mountain ferns of Hawaii.—The origin of peculiar species.—Dr. Hillebrand's views.—Their origin connected not with greater variety of climate in Hawaii, but with isolation.—Summary.

Introductory Remarks

In the endeavour to follow the various stages in the floral history of the Pacific islands from the standpoint of plant-dispersal, a method is here adopted which is not often employed. The usual mode of making a general description of a flora is not intended to bring out its genesis in point of time. We describe the result of a long series of changes dating back to some unknown period, much as one might describe the present condition of a people without reference to their history; and for obvious reasons rarely is an effort made to differentiate the epochs of the stocking of the region with its plants. The difficulties investing such a task in the case of a region situated within a continental area would be almost insuperable. With the oceanic groups of the Pacific such difficulties, though still very numerous, would at all events be fewer in number and less formidable in appearance.

Taking my cue from the well-known instance of Krakatoa, it is here assumed that the earliest epoch is connected with the arrival of the cryptogamic flora (ferns, mosses, lichens, &c.) through the agency of the winds, and with the arrival of the littoral plants

through the agency of the currents. The next era is represented by the genera now peculiar to each group, since it is implied that they have descended from the earliest phanerogams that established themselves in the group. The following epoch, which ends only with the arrival of man, is characterised by the genera found outside the group ; and here different degrees of antiquity are indicated according as the genus is represented wholly or in part by peculiar species, or contains only species found in other regions. The following eight chapters will be devoted to the development of the method here briefly indicated.

The Age of Ferns.

It was established by Dr. Treub in the case of Krakatoa that ferns and algæ formed the earliest vegetation of this island after it had been completely stripped of all its plants in the great eruption of 1883. It is, therefore, but natural that the vascular cryptogams should first be dealt with in any discussion relating to the historical aspects of these floras.

It has been before remarked that the epoch of ferns and lycopods, which began with the earliest stage in the island's floral history, may be regarded as extending to our own day. It is thus implied that the vascular cryptogams of those early times are yet brought there, and that, alike with the littoral plants, these ferns and lycopods have witnessed almost unchanged the great revolutions that have marked the history of the inland flowering plants, more particularly those of the forest flora. This, as I will show, is true in Hawaii, though only in a partial sense in comparison with the other island-groups of Fiji and Tahiti, since in Hawaii nearly half the ferns and lycopods are peculiar to that group, whilst in Fiji and Tahiti not more than 8 or 9 per cent. appear to be endemic. (Rarotonga, according to Cheeseman, possesses one new species amongst its seventy-two ferns and lycopods, and probably in this it is typical of the smaller elevated islands of Eastern Polynesia.)

The large proportion of peculiar Hawaiian species is the central fact in the distribution of vascular cryptogams in the Hawaiian, Fijian, and Tahitian archipelagoes, and indeed in the Pacific islands ; and it is around this fact that much of the following discussion will lie. (For the data relating to the Tahitian region, I have almost exclusively followed Drake del Castillo.)

On looking at the table given below, it will be noticed that whilst there are about the same number of species of ferns and

lycopods in the Tahitian and Hawaiian islands there are at least half as many again in Fiji. When we reflect that the total areas of the Fijian and Hawaiian groups are in each case about 7,000 square miles and that the extent of the whole Tahitian region does not amount to 2,000 square miles, these facts acquire a fresh significance. Ferns and lycopods might, therefore, be expected to figure more largely in the Tahitian flora than in those of Fiji and Hawaii; and this is indeed the case. When we examine the relative proportion of the vascular cryptogams to the indigenous flowering plants in each area we find that whilst in Hawaii they form about 18 per cent. of the total flora and in Fiji not much more than this (see Note 62), in Tahiti they constitute just a third. This excess of vascular cryptogams is reflected in the flora of the outlying groups, the proportion in Rarotonga being, according to Cheeseman, 30 per cent. It is, therefore, evident that in comparison with the other groups Tahiti possesses a marked preponderance in ferns and lycopods. In this respect the Tahitian islands resemble those of Juan Fernandez, where judging from the data relating to the indigenous flora given in Hemsley's *Botany of the Challenger Expedition*, the proportion of vascular cryptogams amounts to between 30 and 38 per cent.

But it has been already implied that the proportion of endemic species of ferns and lycopods is from four to five times as large in Hawaii as it is in Tahiti or Fiji. In Hawaii, therefore, there has been a production of many new species, whilst in Fiji and Tahiti there has been a great rush of immigrants. "Formative energy" in Hawaii (to adopt an expression of Dr. Hillebrand) and "active colonisation" in Fiji and Tahiti, such would appear to be the most conspicuous features in the history of the vascular cryptogams of these three archipelagoes.

In these floras it is, therefore, apparent that respecting the vascular cryptogams the average number of species in a genus does not supply a means of contrasting them. As indicated in the table,

TABLE OF VASCULAR CRYPTOGAMS (FERNS AND LYCOPODS) IN THE GROUPS OF TAHITI, HAWAII, AND FIJI. (See note 63.)

Group.	Number of genera.	Number of species.	Species to a genus.	Number of endemic species.	Percentage of endemic species.	Percentage of ferns and lycopods among the vascular plants.
Tahiti	38	154	4·1	13	8	33
Hawaii	29	155	5·4	70	45	18
Fiji	40	237	5·9	20	8	21

the fern and lycopod floras of Fiji and Hawaii are similar in this respect. Yet in each the average number of species to a genus has a separate significance. A genus may acquire its species through immigration, or they may arise from its formative energy within the particular area. The first principle has been largely dominant in Fiji, the last in Hawaii, and the resemblance between the average number of species in a genus in these two groups is to a large extent accidental. Between the vascular cryptogams of Fiji and Tahiti, however, such a comparison is legitimate; and since the average formative energy is in these groups about the same, the difference is to be attributed to a lessened number of immigrants into the Tahitian area.

The results, so far mentioned, are in the main consistent with the geographical position and the degree of isolation of these three areas. From their proximity to the large continental islands of the Western Pacific, the Fijian islands would have readily received a great number of immigrants from the west, since the intervening sea is not over 500 miles in breadth. They lie in the track of the main line of migration into and across the South Pacific, a track which has been followed by flowering plants and animals as well as by aboriginal man. Assuming that the migration of the vascular cryptogams extended from Fiji eastward to Tahiti, fewer of the immigrants would reach the last-named group. Fewer still would reach the Hawaiian islands, which excluding the groups of low coral islands to the southward are cut off on all sides, whether from the Fiji-Samoan and Tahitian areas, from the coasts of North America, or from the regions north and west, by a breadth of ocean that is never less than 1,500 miles.

That the main track of the ferns and lycopods across the South Pacific to Tahiti has been eastward there can be little doubt. This is indicated in the tables given by Drake del Castillo for Eastern Polynesia, and also by an analysis I have prepared of the distributions that he gives for the species of the Tahitian region (see Note 64). Out of the 154 species there are only two that belong exclusively to the American side of the Pacific; whilst 58 are derived exclusively from the Asiatic side, and mainly from Indo-Malaya. The drift of the ferns and lycopods eastward from Fiji is also brought out in the number of Tahitian species common to Hawaii and Fiji. Of these about 76 per cent. are common to Fiji or to the groups around, and only 30 per cent. occur in Hawaii. The Tahitian species found in Hawaii occur also in Fiji with the exception of two or three mountain species which have doubtless failed

to find a suitable elevation in Fiji. These two or three mountain ferns and lycopods are probably the only vascular cryptogams possessed in common by Hawaii and Tahiti to the exclusion of other groups. (See Note 64.)

The prevailing Indo-Malayan origin of the ferns and lycopods of the archipelagoes of the Fijian area (Fiji, Tonga, Samoa) is so well established in the writings of Seemann, Baker, Hemsley, Christ, and Burkill that there is no necessity to enter into details here. That the stream of vascular cryptogams to Hawaii has proceeded mainly from the Old World side of the Pacific is shown in the circumstance that of the eighty and odd species found outside the group nearly half are from the Asiatic side exclusively and only three from America alone, whilst about a fourth occur in both continents, and a fourth are confined to Polynesia. One point, says Dr. Hillebrand, comes out in strong relief, and that is "the great number of ferns scattered over the long track which leads from the Hawaiian islands through Polynesia and Malaysia to the east coast of tropical Africa." But he adds significantly that "it cannot be inferred from this fact that all the species in question have travelled eastward to find the terminus of their long migration on this group, unless the principle be established, that the formative energy of a species or genus be greatest at the circumference or farthest extremity of its area" (p. 542).

Though evidently prepared to admit the general eastward trend of plants in the Pacific, Dr. Hillebrand (p. xxviii) puts forward in the case of the ferns the startling view that originally spores of a few simple species have been diffused over various countries and that they have there evolved on parallel lines "predetermined by the structure of the original immigrant" a series of higher forms, so that the same form might have been produced in two widely distant localities, as, for instance, in Ceylon and Hawaii. The editor, Mr. W. F. Hillebrand, gives good reasons for his belief that this does not represent the matured opinion of the author. It is, however, worth noting in this connection that Dr. Karl Mueller has advanced a similar view with respect to the lower orders of plants. (See a translation of his paper in *Trans. and Proc. N. Z. Inst.* Vol. 25.) Bearing in mind the known capacity of ferns for dispersal by the winds, an hypothesis of this kind, even if established, seems scarcely needed in the study of fern-dispersal.

It is probable that many of the ferns and lycopods reached

Hawaii directly and not through South Polynesia. The mountain-ferns of this group could hardly have been received by that route, since, as is shown below, they do not as a rule occur in that region.

Some other interesting relations present themselves in connection with the Hawaiian ferns and lycopods when we consider the distribution of its non-endemic species in the other two groups of Fiji and Tahiti. Out of these species, some eighty in all, not more than half are common to all three groups, and about two dozen have not been found either in Fiji or in Tahiti. Of these last quite half are mountain species in Hawaii, having their station at elevations exceeding those of the highest districts of Fiji and of the several islands of the Tahitian area, excepting the limited region comprised in the uplands of Tahiti itself.

A glance at the list, given in Note 65 of some of the mountain ferns of Hawaii not recorded from Fiji and Tahiti will show that these species are very widely distributed. Ferns .and lycopods found in the Himalayas and in the Andes meet on the higher slopes of the lofty mountains of Hawaii and in no other of the less elevated island-groups of the open Pacific. This distribution of the vascular cryptogams thus foreshadows a principle that will come into prominence in the case of the flowering plants, namely, that difference in elevation has been an important factor in determining some of the contrasts between the Hawaiian, Fijian, and Tahitian floras. The contrasts here implied are those connected with the climatic conditions of station, since several plants of temperate regions, such as Aspidium filix mas, Asplenium trichomanes, Asplenium adiantum nigrum, &c., that are at home in the highlands of Hawaii, do not occur in either Fiji or Tahiti. We can infer that widely ranging ferns and lycopods have been dispersed over the oceanic groups of the tropical Pacific with a fair degree of uniformity, and that any marked contrasts in their distribution may be attributed to considerable differences in the altitude of the islands.

In appreciating such a conclusion, and in dealing with apparent exceptions to the rule, the relation between the vertical range of a species and its lateral distribution has to be considered. We find, for instance, that whilst the Common Bracken (Pteris aquilina) is a mountain plant in Hawaii, it occurs also in Fiji and Tahiti. Since, however, it is found all over the temperate and tropical regions, and has a vertical range in Hawaii of from 800 to 8,000 feet, any difficulty in this respect is thus explained.

Aspidium aculeatum, a characteristic fern of temperate latitudes, seems at first to present a difficulty, which, however, proves to be more apparent than real. Whilst it has been recorded from Hawaii at heights of 6,000 to 9,000 feet, and from Tahiti at 4,000 feet, it has also been found in Fiji and Samoa; but since it was not collected by Seemann in Fiji, it can scarcely be common, and Horne seems only to have obtained it from the tops of mountains in Vanua Levu at an elevation of 1,800 feet.

Up to this point the non-endemic ferns and lycopods have been chiefly discussed. We will now briefly deal with the probable cause of the relative preponderance of peculiar or endemic species in Hawaii as contrasted with Fiji and Tahiti. In this respect the Hawaiian islands, as remarked at the commencement of this chapter, come into sharp contrast with the other two groups; but it would seem that the differentiation has rarely acquired a generic value (see Note 66). In this respect the age of ferns is markedly distinguished from the succeeding era, the age of the arborescent Compositæ and of Tree-Lobelias, to which a large number of peculiar genera belong. This, according to my view, is to be attributed to the circumstance that whilst the dispersion of spores by the wind is probably as active in our own time as it was in the earliest stage of the floral history of Hawaii, the dispersion of seeds by birds, to which the flowering plants in the main originally owe their presence in this group, has been greatly influenced by the various changes that have affected the migration of birds over the Pacific, a subject discussed in later pages.

Respecting the origin of the species of ferns and lycopods peculiar to Hawaii, it is first of importance to quote the remarks of Dr. Hillebrand on the subject. Speaking of the whole flora (p. xxv), but evidently with the ferns more especially in his mind, he says:—"Nature here luxuriates in formative energy. Is it because the islands offer a great range of conditions of life? Or is it because the leading genera are in their age of manhood, of greatest vigour? Or is it because the number of types which here come into play is limited, and, therefore, the area offered to their development comparatively great and varied?" It is deeply to be regretted that sickness and death intervened before the author was able to give to the world his matured views on the very important points here raised. Yet they are much the same questions that man is ever putting to the life around him. There is the same querulous note that we find in all, the question that begins, the question that ends, and the reply that never comes.

"The evolution theory (writes Dr. Hillebrand, p. xxix) could hardly find a more favourable field for observation than an isolated island-group in mid-ocean, large enough to have produced a number of original forms, and at the same time so diversified in conditions of temperature, humidity, and atmospheric currents as to admit an extraordinary development in nearly every direction of vegetable morphology, uninfluenced by intercrossing with foreign elements." Isolation thus admittedly offers the preliminary determining or favouring conditions. This is directly indicated by the fact that Hawaii possesses fewer genera of ferns and lycopods than either Fiji or Tahiti, notwithstanding that it has the same area as Fiji, and is in extent three or four times the size of the whole Tahitian area. One effect of isolation in Hawaii has, therefore, been greater room for the development of new forms. It has, however, already been remarked that the islands of the Fijian area are much less isolated than those of the Hawaiian group, and that in consequence the free immigration possible in the one group has been checked in the other. Fiji possesses in respect to vascular cryptogams at least half as many species again as Hawaii, but Hawaii has three or four times the number of peculiar species. Yet before this great contrast can be ascribed to different degrees of isolation, it is necessary to exclude another possible cause presented by the greater range of life-conditions in Hawaii. It is possible that all the Hawaiian peculiar species may belong to the higher levels, elevations, as before shown, not represented in the Fijian islands, which correspond only to the lowlands of Hawaii, that is, to levels below 4,000 feet. If this is the case, the contrast between Fiji and Hawaii would be connected mainly with a difference in life-conditions, and, however potent the isolating influences might have been in Hawaii, they could hardly have been concerned with this striking difference.

In order to determine this point, I went carefully through the account given by Hillebrand of the Hawaiian ferns and lycopods, noting the altitudes there given, and making use of the maps and of my own local knowledge of the islands of Oahu and Hawaii, where the elevation is neither directly nor indirectly implied. As a result, I found that out of sixty-six endemic species available for my purpose, forty-seven had their stations at levels below 4,000 feet, that is in the region corresponding to Fiji, and nineteen at elevations exceeding this height. This, however, did not finally decide the question, since the proportion of endemic species may be much smaller in the region below 4,000 feet than in that above it. I,

therefore, went over the ground again, and found, as shown in the table below, that the percentages of peculiar species amongst the total available for my use were not very far apart, 58 per cent. for the upper region and 43 per cent. for the lower region.

DISTRIBUTION OF THE HAWAIIAN FERNS AND LYCOPODS ABOVE AND BELOW 4,000 FEET.

	Number.	Endemic.	Percentage of endemic species.
Species below 4,000 feet	110	47	43
,, above ,, ,,	33	19	58

From the above it would appear that although the process of species-production in the Hawaiian islands has seemingly been rather more active above than below 4,000 feet, if we were to compare the entire vascular cryptogamic flora of Fiji with that of the corresponding lower levels of the Hawaiian group we should obtain much the same contrast in the proportion of peculiar species that we obtained when comparing all the ferns and lycopods of both groups. In other words, if we were to restrict our comparison with Fiji, and I may add Tahiti, to that lower portion of Hawaii that corresponds in elevation, we should not get results very different from those to be obtained by including the Hawaiian upland regions as well.

We are, I think, on these grounds justified in assuming that the relatively great development of new species of ferns and lycopods in Hawaii as contrasted with Fiji is not to be connected with the greater elevation of those islands. The only thing that we have been able to associate with the greater altitude of the Hawaiian Islands, and the consequent greater range of climatic conditions, when contrasting the Fijian and Hawaiian vascular cryptogams, is the occurrence of a number of peculiar mountain species and of wide-ranging temperate species that are found in the uplands of Hawaii, but not in the less elevated islands of Fiji.

On the whole, therefore, it is to be inferred that the greater display of formative power among the ferns and lycopods of the Hawaiian Islands is in great part to be associated with the isolation of this group as compared with those of Fiji and Tahiti. The indications supplied by the vascular cryptogams resemble in kind those we shall obtain from the study of the flowering plants, but there is this important distinction. In formative power, as shown

in the development of new specific and generic types, the Hawaiian vascular cryptogams are far exceeded by the flowering plants where the proportion of endemic species amounts to 80 per cent. We have no reason to believe that the winds, to which the ferns and lycopods chiefly owe their dispersal, are less effective now in carrying their spores than they were in the earliest era of the floral history of Hawaii or in the intervening periods. In the course of ages the winds have been more uniform in their action as plant-dispersers even than the currents, and certainly far more than birds.

On the other hand, in the case of the Hawaiian flowering plants that depend on the varying influence of the migrant bird, the agency of dispersal has often been suspended altogether, and far greater differentiation or departure from the original type has resulted, the amount of change often reaching to the value of a generic distinction. It is a question, however, whether the isolation of the Hawaiian Islands is to be entirely connected with their mid-oceanic position. It will be shown in Chapter XXXIII. that effects almost as great have been produced in continental regions and in continental islands, and that the isolated situation of Hawaii has not induced but has intensified these results. In the later eras of plant-life a process of segregation has been ever active throughout the tropical world whether in the case of an elevated oceanic island or of a mid-continental mountain.

The following are some of the principal points that have been emphasised in the foregoing discussion of the ferns and lycopods of the Hawaiian, Fijian, and Tahitian Islands :—

(*a*) In all three groups the vascular cryptogams (ferns and lycopods) have been largely supplied from the warmer regions of the Old World. But whilst in the South Pacific the migration has been mainly from Fiji eastward to Tahiti, it is probable that Hawaii in the North Pacific has been in part independently stocked.

(*b*) Whilst in Hawaii many peculiar species of ferns and lycopods have been developed, in Fiji and Tahiti there have been comparatively few.

(*c*) Whilst there has been more or less free immigration into Fiji and Tahiti there has been comparative isolation in Hawaii. Though the areas of the Fijian and Hawaiian archipelagoes are about the same, Fiji possesses at least half as many species again as Hawaii ; but Hawaii owns three or four times the number of peculiar species.

(*d*) Though the land-area of the Tahitian region does not

exceed a fourth part of that of Hawaii, it has the same number of species. The Tahitian islands therefore display a predominance of ferns and lycopods.

(*e*) The non-effective influence of the greater elevation of the Hawaiian Islands on its preponderance of peculiar species is shown by comparing all the ferns and lycopods of the Fijian and Tahitian Islands with those of the corresponding lower levels of the Hawaiian Islands, when we find much the same contrast exhibited in the number of peculiar species.

(*f*) Whilst a large proportion of the ferns and lycopods are common to all three groups, Hawaii possesses a number of mountain species, widely distributed in temperate regions and on the higher levels of mountainous areas in the tropics, that are not found either in Fiji or in Tahiti. Their absence from these two groups is due to the insufficient elevation of the islands and to the non-existence there of extensive areas of any altitude.

(*g*) The agency of the winds in dispersing the spores of ferns and lycopods has been relatively uniform through the ages when compared with the varying agency of the migrant bird, to which the flowering plants mainly owe their distribution. Thus it is that in the Pacific islands the vascular cryptogams have experienced much less differentiation than the flowering plants, though as a rule far older denizens of the islands. Yet we cannot doubt that the same principle has been at work in both cases, the difference arising in the instance of the flowering plants from the interrupted and often suspended agency of birds in the work of dispersal.

(*h*) It is a question whether there is not something more concerned in the isolation of the Hawaiian group than its mid-oceanic position, since effects almost as great have been produced in continental regions.

CHAPTER XXI

THE ERAS OF THE FLOWERING PLANTS

THE AGE OF COMPOSITÆ.

The islands of the tropical Pacific as the homes of new genera and new species.—The significance of a large endemic element.—Synopsis of the eras.—The era of endemic genera.—The endemic genera of Compositæ.—Their affinities and mode of dispersal.—The mystery of the suspension of the dispersing agencies.—Mr. Bentham's views.—The remnant of an ancient Composite flora in the tropical Pacific.—The dispersion of the Compositæ antedates the emergence of the island-groups of the Fijian region at the close of the Tertiary period.—Summary.

The Endemism of the Pacific Island Floras.

As far as the production of new species is concerned, the Hawaiian group presents the same contrast with the Fijian and Tahitian groups in respect of the flowering plants that it does as regards the ferns and lycopods. The proportion of endemic species, after excluding all introduced plants, is in Hawaii 80 per cent., in Fiji about 50 per cent., and in Tahiti 35 per cent. (see Table A). The same contrast is also displayed in the number of peculiar genera. In Hawaii there are, according to Dr. Hillebrand, 37 or 38, and in Fiji Dr. Seemann discovered 16; whilst, as we learn from Drake del Castillo, there are only 3 or 4 in the Tahitian Islands. (As will be pointed out later on, these numbers for Fiji and Hawaii have to be reduced, but the general inference to be drawn from them is not materially affected ; see Table B.)

But if we look at the accompanying table (Table B) we notice that the flora of Hawaii is sharply contrasted with those of Fiji and Tahiti not only in the large proportion of endemic genera, but also in the large number of non-endemic genera with peculiar

species, and in the small proportion of genera possessing no peculiar species. There is an endemic element of greater or less degree in about 70 per cent. of the Hawaiian genera, whilst in Fiji only about 53 per cent. and in Tahiti as few as 34 per cent. of the genera contain to a varying extent peculiar species. Another feature brought out in this table is the relative poverty of genera in the Hawaiian Islands. Fiji, though about the same size as Hawaii, contains nearly half as many genera again, whilst the islands of the Tahitian region, which in the aggregate amount to only one-third or one-fourth of the area of the islands of Hawaii, possess nearly as many genera.

TABLE A (FLOWERING PLANTS).

Proportions of Endemic Species in the Hawaiian, Fijian, and Tahitian floras, with those for Samoa, Tonga, and Rarotonga added.

Groups.	Number of species.	Number of endemic species.	Percentage of endemic species.
Hawaii	686	546	80
Fiji	S. 617 H. 1086	288 620	47 57
Tahiti	315	112	35
Samoa	326	110	34
Tonga	285	17	6
Rarotonga Island ...	140	17	12

Remarks.—The materials for this table have been obtained from the works of Hillebrand for Hawaii, Seemann and Horne for Fiji, Drake del Castillo for Tahiti, Reinecke for Samoa, Hemsley and Burkill for Tonga, and Cheeseman for Rarotonga. The two estimates for Fiji are marked S. for Seemann and H. for Horne, the last being a rough preliminary computation made by Horne himself.

The results given are only to be considered as approximations liable to emendation, but as regards the proportion of endemic species in the several groups they no doubt illustrate fairly well the relative degree of endemism in the various archipelagoes. The results for Samoa, Tonga, and Rarotonga are merely added in order to enable a comparison to be made with sub-groups of a

region and with solitary islands, the Hawaiian, Fijian, and Tahitian groups being regarded as the three principal centres of plant-life in the open Pacific.

All plants introduced by the aborigines and the white man are excluded. In so doing, I have mainly followed Seemann, a safe guide in all matters relating to weeds and to cultivated plants. The flora of a Pacific island thus treated undergoes serious diminution in its extent. In the case of the Rarotonga flora, for example, which according to Cheeseman includes about 260 flowering plants, the number of truly indigenous plants, in the sense here implied, is only 140. Though this is an extreme case, it will serve to illustrate the principle here followed.

TABLE B (FLOWERING PLANTS).

Comparison of the Hawaiian, Fijian, aud Tahitian genera. (All genera containing introduced plants entirely are excluded.)

Group.	Non-endemic genera.			Endemic genera.	Total.
	No endemic species.	Some species endemic, some not.	All species endemic.		
Hawaii	70 (31)	30 (13)	95 (43)	28 (13)	223 (100)
Fiji	S. 150 (47) H. 162 (47)	S. 74 (23) H. 80 (23)	S. 87 (27) H. 94 (27)	S. 10 (3) H. 10 (3)	S. 321 (100) H. 346 (100)
Tahiti .... (Eastern Polynesia)	125 (66)	21 (11)	40 (21)	4 (2)	190 (100)

Remarks.—The figures in brackets are percentages. S. = Seemann, H. = Horne and Seemann.

In the construction of this table, Hillebrand, Seemann, and Drake del Castillo have been mainly followed, except with regard to the endemic genera for Hawaii and Fiji. In this respect the *Index Kewensis* has been largely consulted as well as Engler's publications, as indicated in the text. Hillebrand's total of nearly forty Hawaiian peculiar genera and Seemann's total of sixteen for Fiji have thus been considerably reduced. The two results given for Fiji are those of Seemann alone and with Horne superadded. Horne discovered, according to Hemsley, no new genera, but several genera from outside regions were added to the Fijian flora. Taking them as twenty-five (two-thirds of his own computation), I have

apportioned them as in Seemann's results. The Tahitian region here includes Eastern Polynesia.

It is necessary before proceeding further to obtain a correct idea of the significance of a large endemic element in the phanerogamic flora of a Pacific archipelago. We have therefore at the outset to inquire whether it is indicative of isolation or of antiquity. If the number of peculiar genera is to be regarded as the test of the relative antiquity of different Pacific floras and, by implication, of the islands to which they belong, these three groups, as shown in Table B, would arrange themselves in the following order, namely, Hawaii, Fiji, Tahiti. This test might be reliable if the several groups were in the same condition of isolation. Since, however, as we have previously seen, the Fijian Islands still enjoy a fairly free communication with the islands westward, whilst the Hawaiian group is largely cut off, it is apparent that the tendency to generic differentiation in Fiji might have been often swamped by immigration, and that Fiji with its much smaller number of endemic genera may even be older than Hawaii. This objection does not apply quite as forcibly to a comparison between Hawaii and Tahiti, yet for reasons before given it may be regarded as sufficient to negative any inferences concerned with relative antiquity.

On account, therefore, of the great differences in the degree of isolation of these three groups, we cannot be guided in our estimation of the relative antiquity of their floras by their number of peculiar genera. With the evidence at our disposal we are compelled to accept the view, which indeed a single glance at a map would suggest, that the number or proportion of endemic genera is to be connected with the degree of isolation. Whether a parallelism can be traced in the original stocking of these groups with their earliest flowering-plants is a matter that can only be elucidated by a further analysis of the peculiar genera.

Synopsis of the Eras of the Flowering Plants in the Tropical Pacific.

A. *The Era of the Endemic Genera.*—Mostly American in their affinities. Represented particularly by Compositæ and Lobeliaceæ.

B. *The Era of Non-Endemic Genera.*

(1) The mountain genera, either cosmopolitan in temperate latitudes or derived from the New Zealand or the Antarctic flora. Mostly represented in Hawaii.

(2) The genera forming the low-level flora of Hawaii below 4,000 or 5,000 feet and composing almost the entire floras of the Fijian and Tahitian regions. Predominantly Indo-Malayan.

(*a*) The age of general dispersal over the tropical Pacific, the genera with only peculiar species being first treated, and afterwards those possessing a non-endemic element.

(*b*) The age of local dispersal over the tropical Pacific.

THE FIRST ERA OF THE FLOWERING PLANTS, BEING THE AGE OF THE ENDEMIC GENERA.

With the above preliminary remarks I pass on to the next stage in the history of the stocking of these islands with their plants. The age of the ferns and lycopods is left behind, and it is assumed that the next era is mainly indicated by those genera of phanerogams that are now peculiar to their respective groups. In this connection by far the most interesting of the three regions, the Hawaiian, the Tahitian or East Polynesian, and the Fijian, is that of Hawaii, which, as before observed, is distinguished from the groups of the Fijian and Tahitian regions, or, in other words, from all the oceanic archipelagoes of the tropical Pacific, by its large number of endemic genera.

Peculiar genera of shrubby and arborescent Compositæ and of arborescent Lobeliaceæ form the most striking characteristics of the endemic genera, and therefore of the ancient flora of Hawaii. It is in this connection of singular interest to remark that of the three endemic genera of the Tahitian flora one is an arborescent genus of the Compositæ, and the other two are shrubby genera of the Lobeliaceæ. There are, therefore, indications here of an ancient insular flora of the Pacific, characterised mainly by the prevalence of Compositæ and Lobeliaceæ. It is, however, remarkable that not only are no endemic genera of these orders known from Fiji or from the adjacent groups of Samoa and Tonga, but that the Lobeliaceæ are not represented at all, whilst amongst the Fijian Compositæ, with the exception of Lagenophora, the genera display no endemic element as far as the data at my disposal indicate.

The problem we are brought face to face with is clearly stated by Mr. Hemsley in the *Introduction to the Botany of the Challenger Expedition* (p. 68). "In Polynesia as elsewhere," he remarks, "the Compositæ more particularly are perplexing to the

botanical geographer, for although they have their greatest affinities in America, as well as the sub-arboreous Lobeliaceæ, so numerous in the Sandwich Islands, yet the bulk of the vegetation seems to have been derived from the Australo-Asiatic region."

In attempting to approach this problem I do so from the standpoint of dispersal. There are so many intricate questions bound up with the systematic position of these genera that in dealing with them the student of plant-distribution would require the capacities and opportunities of the eminent botanist who dealt with the distribution of ten thousand species of Compositæ. On such ground, therefore, and only under the guidance of others, I will lightly tread.

The Endemic Genera of Compositæ.

On account of their endemic character the peculiar genera of Compositæ are regarded as belonging to the oldest era of the flowering plants of the island-groups lying in the tropical latitudes of the open Pacific. This is the view of Bentham, but it is, of course, the opinion that most botanists would arrive at with the facts before them. With the exception of the solitary Tahitian genus Fitchia, they are all restricted to the Hawaiian Islands, and nearly all are either shrubby or arborescent, the greatest height of 25 to 30 feet being attained in the Tahitian genus and in Hesperomannia of Hawaii.

Nine Hawaiian genera are included in this era, though, strictly speaking, we ought only to concern ourselves with the six genera, Remya, Argyroxiphium, Wilkesia, Dubautia, Raillardia, and Hesperomannia, since the other three, Tetramolopium, Lipochæta, and Campylotheca, are only on the borderland of generic distinction. It is, however, necessary that we should include these three genera in our treatment of the Hawaiian endemic genera, more especially because they appear to have been the last arrivals of the early Compositæ. They still display, as shown below, a very suggestive connection with the land of their birth, a circumstance that is of much importance in finally determining the source of the other strictly endemic genera, where the links with their original homes have been in most cases largely severed.

It would, however, be quite out of place here to enter into any details into the affinities of these Hawaiian genera of Compositæ, and I will limit myself here to such general conclusions as may be derived from the pages of Bentham, Hillebrand, Hemsley, and

other writers, and such as are in accordance with the facts of distribution given in the *Index Kewensis.* Most ancient of all are the genera Remya, Argyroxiphium, Wilkesia, and Hesperomannia, which, although belonging to tribes that only occur on the American continent, as in the Mexican region, stand quite isolated, and, as Dr. Hillebrand remarks, probably belong to the oldest denizens of the Hawaiian Islands. It is noteworthy that these four ancient genera only contain two species apiece, a circumstance that favours their priority in point of age.

The American affinities, however, are not always of the character that we might have expected. Thus, it was remarked by Mr. Bentham that although the tribe Mutisiaceæ attains a great development in South America, and especially in Chile, its only representative in the Pacific islands is the very rare arboreous Hesperomannia of Hawaii.

Rather less isolated in character, and we would presume therefore of somewhat less antiquity, are the two closely allied genera of Raillardia and Dubautia, which have a close relative in Raillardella of the Sierra Nevada in California. Then we come to the three genera, Tetramolopium, Lipochæta, and Campylotheca, that, being still in touch with the world outside, may be regarded as the latest arrivals of the early genera of the Compositæ. Tetramolopium, concerning which botanists were unable to agree, would seem, according to the *Index Kewensis*, to possess Mexican and Ecuadorian as well as Hawaiian species. Lipochæta, nearly related to other American genera, contains a dozen species, of which eleven are found only in Hawaii, whilst the twelfth occurs, according to the *Index Kewensis*, in California, and, according to Dr. Hillebrand, in the Galapagos group. Of the generic value of Campylotheca there seems a doubt, and its distinctness is scarcely recognised in the *Index Kewensis.* It is, however, closely allied to Coreopsis, an American genus represented, according to Drake del Castillo, in the Marquesas.

In the Tahitian region, that is to say in Eastern Polynesia, the genus Fitchia alone belongs to the early age of the Compositæ, so characteristic of Hawaii. Indications of the former widespread range of the genus over this region of the South Pacific are afforded by its being now represented by two species in Tahiti and by one species in Rarotonga, localities nearly 700 miles apart. It was thus regarded by Bentham, who saw in it a solitary remnant of the ancient South Pacific flora. Like the Hawaiian genera, as shown below, it is often restricted to the higher levels. Botanists differ

about its affinities, and a discussion of the subject will be found on pages 20 and 66 of the *Introduction to the Botany of the Challenger Expedition.*

The restriction of these ancient genera of the Polynesian Compositæ to the upland regions is of some interest. "The preponderance of Compositæ among the high-level plants obtains almost throughout the world." This observation was made by Mr. Hemsley in connection with the flora of the highlands of Tibet (*Journ. Linn. Soc. Bot.* vol. 35, 1902), where the Compositæ constitute about 19 per cent. of the flowering plants; and I may remark in passing that, according to Mr. Ball, one of the most conspicuous elements in point of frequency in the higher flora of the Great Atlas is presented by the Compositæ which make up between 12 and 13 per cent. of the whole flora (Hooker and Ball's *Marocco aud the Great Atlas*). This feature of alpine floras is brought into great prominence in Schimper's recent book on Plant Geography.

Some of the most lasting reminiscences that the naturalist will bear away with him from the highlands of Hawaii are connected with the Compositæ. Those who have ascended the mountains of Mauna Kea and Mauna Loa, will remember that amongst the last plants occurring above the forest zone, and scattered about on the ancient lava fields at elevations exceeding 10,000 feet above the sea, are species of Raillardia and the beautiful "Ahinahina" (Argyroxiphium). It is, however, in the open, scantily wooded region, elevated 6,000 to 9,000 feet, and lying between the true forest zone below and the bare lava slopes above, that the shrubby and arborescent Compositæ of the large island of Hawaii are most at home. Such regions, as Hillebrand well describes (p. xxiv), are characterised by stunted trees, chiefly Sophora, Cyathodes, Myoporum, and others, associated with arborescent Raillardiæ of the order of Compositæ. Between them luxuriate other shrubby Compositæ of the genera Raillardia, Dubautia, Campylotheca, and Artemisia, together with Strawberries, Raspberries, and species of Vaccinium.

Botanists have not given us much account of the associates of the interesting genus Fitchia on the uplands of Tahiti. We learn, however, from Nadeaud that in his time these Composite trees and shrubs were spread over the higher region of the island of Tahiti above 800 and 1,000 metres. Cheeseman, to whom we are indebted for the discovery and the description of the Rarotongan species, tells us that this tree, which attains a height of 25 feet in the sheltered valleys, and is much dwarfed on the exposed ridges and

hill-tops, often forms the greater part of the forest above 500 feet, and reaches the highest peaks of the island (2,250 feet).

In discussing the probable mode of dispersal of these early Composite plants of the Pacific we shall be treading on somewhat debatable ground. We will, however, point out that the mere possession of structures that could be utilised for dispersal of the seeds is not the only important question here involved. If we could demonstrate that all these genera possess exceptional capacities for distribution over the ocean, we should prove too much, since the process has been in the main suspended for ages. If, on the other side, it could be shown that their fruits are not at all suited for such dispersal, we should prove too little, since the ancestors of these genera must have been transported to these islands in some fashion or other. This clearly indicates that other important factors have also come into play in determining the distribution of the early Compositæ of the Pacific islands.

It was long ago pointed out by De Candolle that the possession of a pappus does not, as a rule, increase the area of a Composite plant, although as regards hooks and barbed appendages, such as occur in Bidens, the greater areas of the plants thus provided may be, as he thought, in some measure explained. Even in respect to hooks and barbs it would be easy to point to cases where, as Bentham remarks, unusual powers of adherence are by no means indicative of wide dispersal in all cases. In any event it will be also incumbent on us to explain why these genera no longer possess facilities for distribution. This suspension of the means of dispersal is not, however, peculiar to the age of the endemic genera of the Pacific islands. It is a character but in a less degree of the succeeding age, the age of genera found outside the group, but represented within it by endemic species ; and from this we may suspect that we have had in operation in the Pacific an influence, far-reaching both in time and space, to which the agencies of dispersal have been compelled to adapt themselves, an influence which has acted as a distributor of the distributing agencies.

Coming to the fitness for dispersal of the achenes of the early Composite genera of the Pacific islands, it will be assumed that they have been, as a general rule, transported in birds' plumage. The fruits are usually 2·5 to 12 millimetres ($\frac{1}{10}$ to $\frac{1}{2}$ inch) in length, and are provided either with a pappus of soft or stiff bristles, or with awns or teeth, but these appendages vary much in size in the different genera and in different species of the same genus. The instance of Lipochæta is especially significant as indicating the

alterations which the appendages of the achene may have undergone in the cases of other genera. With most species there are usually two or three teeth or short awns, but in some species these are obsolete, and in others they are long and stout.

Bearing these facts in mind we should hesitate to rely too much on the present condition of the achenes in the other genera as an indication of the fitness for dispersal of the fruits of their ancestors. In one genus, Campylotheca, which may be regarded as among the youngest of the genera, the achenes are provided with barbed or hooked awns which cause them to adhere as tenaciously to one's clothes as in the case of those of Bidens, an allied genus. In Fitchia, the Tahitian genus, which may be looked upon as one of the oldest of the Pacific genera of Compositæ, the achene is furnished with two long awns or setæ, which, as Drake del Castillo observes, recall those of Bidens. The achenes of the other Hawaiian genera, as regards their fitness for dispersal in plumage, may be said to give less definite indications. In some, as in Dubautia and Raillardia, there is a typical pappus of ten to twenty long hair-like bristles. In others again, as in Wilkesia and Argyroxiphium, the pappus is much reduced, and in some species of Lipochæta it is, as above remarked, quite obsolete.

The chances of the achenes of the parent plants having in some cases been originally transported to the islands in the plumage of birds would be increased by a bird making its nest of the plant-materials or amongst the plants themselves, or by its pecking at the fruit-heads. In our own time different species of the grouse family on the slopes of the Californian and Columbian mountains make their nests on the ground under the shade of Artemisia bushes and find a portion of their sustenance in their fruits. Artemisias also form one of the features of the vegetation of the Hawaiian uplands; but since they present only specific differentiation they are referred to a later era. Yet it will be on the slopes of the Rocky Mountains and of the Californian Sierra Nevada, amongst the "sage-brush" and the grouse, that we may have to stand when we look in thought across the Pacific towards far distant Hawaii and ask ourselves whence came its tree-like Raillardias, its shrubby Dubautias, its tall Wilkesias, and the silvery Ahinahinas (Argyroxiphium).

It is possible that in some genera the achenes have, or had, a means of adhering to plumage through a "sticky" secretion, such as is sometimes found with Lagenophora, an Hawaiian genus of the next era, and also with the weed-plant Adenostemma viscosum;

but this is a point that has not yet been investigated. Nor can we altogether exclude the chance of the achenes having in some cases been transported unharmed to Hawaii in a bird's stomach. The possibility of this has been above implied in the case of Artemisia; and it is pointed out in Chapter XXXIII. that pigeons in Hawaii feed sometimes on the achenes of Compositæ. The Hawaiian goose (Bernicla sandwicensis) lives, according to Mr. Dole, on Sonchus asper, an introduced plant, as well as on berries (Wilson's *Aves Hawaiiensis*). There are numerous references of this nature in books about birds, and it should always be remembered that birds in pecking at the fruit-heads scatter the seeds on their feathers. (See Note 67.)

From the foregoing remarks it may, I think, be inferred that the achenes of the ancestors of the original Composite genera of the Pacific islands were in all probability not unfitted for transport by birds, more especially in their plumage. Some of my readers, however, may express a doubt as to whether birds likely to disperse seeds would be found in any numbers at the great heights where some of the continental Compositæ occur. But it is well known that birds of the grouse and partridge family frequent high levels in continental regions over much of the globe. Arborescent Compositæ are found at heights of 10,000 to 14,000 feet on the mountains of Central Africa; and it should be noticed that Sir Harry Johnston observed "francolins" on the slopes of Ruwenzori up to 13,000 feet (*Uganda Protectorate*, vol. 1; *Trans. Linn. Soc. Bot.*, Ser. II. vol. 2). Sir Martin Conway in the Bolivian Andes found geese, ducks, gulls, snipe, &c., numerous in suitable places up to 17,000 feet (*Journ. Roy. Geogr. Soc.*, 1899); whilst geese and teal were noticed by Sir Joseph Hooker and others at elevations of 17,000 feet in the mountains of Tibet (Hooker's *Himalayan Journals; Journ. Linn. Soc. Bot.*, vol. 35, p. 147). These are all birds, as shown in Chapter XXXIII., that are likely to disperse plants, and probably none more effectually than the goose, of which Hawaii possesses a particular variety or species. It may be remarked that geese, ducks, gulls, and other birds use Cotula plumosa in Kerguelen for making their nests (Dr. Kidder quoted by Mr. Dixon in his book on Birds' Nests).

Sea-birds were probably the principal agents in carrying the achenes of the early genera of the Compositæ to Hawaii. Dr. Hillebrand attached importance to the tropic-bird (Phaethon) in the distribution of species (Introd., p. 30); and since these birds breed at the crater of Kilauea in Hawaii, 4,000 feet above the sea,

and also high up in Tahiti (Moseley), its agency is not unlikely. I am inclined to think, however, that birds like the petrels and puffins, that in nesting burrow in the ground, choosing places where the vegetation is thickest, and where they would be likely to get seeds on their feathers, would be more efficient agents. This is the view expressed by Prof. Moseley in Wallace's *Island Life*, p. 250. He considered that albatrosses, petrels, and puffins have played a great part in the distribution of plants, and to some degree especially account for the otherwise difficult fact that widely distant islands in tropical seas have similar mountain plants. Birds, he says, that in high latitudes, as at Tristan da Cunha and Kerguelen, often burrow near the sea-level, in the tropics choose the mountains for their nesting-place; and he refers to a puffin that nests on the top of one of the high mountains of Viti Levu at an altitude of 4,000 feet, to a petrel nesting among ferns at Tahiti at an elevation of 4,400 feet, and to another petrel breeding in like manner in the high mountains of Jamaica at a height of several thousand feet above the sea. He gives point to these interesting remarks, which might be supplemented by data from other parts of the world, by observing that it is not necessary that the same species should now cover the range of the plants concerned. The ancestor of the species might have carried the seeds, and the range of the genus is alone sufficient. It may be added that, as I have shown in Chapter XXXIII., sea-birds have been far more active agents in the distribution of plants than many people might imagine. The more recent observations of Ekstam in Spitzbergen have thrown considerable light on this subject.

Having in the first place formed the opinion that the achenes of the early Hawaiian Compositæ are suited for dispersal by birds, and then shown that sea-birds were probably the principal agents, we are met with the curious difficulty that in the case of the early Hawaiian genera of Compositæ the complete suspension for ages of the means of dispersal is involved in the circumstances that these genera are confined to the Hawaiian group. We can attribute to the agency of existing sea-birds the occurrence of the genus Lagenophora in the uplands of Hawaii, on the mountain-tops of Fiji, and in Australia and New Zealand; but the agency of birds as at present in operation does not assist us except indirectly in the case of the genera restricted to Hawaii or to Tahiti. Is it possible, we may inquire, to penetrate this mystery? Why, we may ask with Mr. Hemsley, has the agency ceased acting, and why have its operations been confined to the conveyance of seeds *to*

the islands and not *from* the islands as well (*Intr. Bot. Chall. Exped.*, p. 66)? I need scarcely add that the same question presents itself with all the other peculiar genera of these islands, and in fact with endemic genera all over the world. What can be stranger, it may be remarked, than the limited distribution of the Pandanaceous genus Sararanga in the Western Pacific, although suited for dispersal by frugivorous birds. This is not, indeed, a special difficulty connected with oceanic islands; it applies to the whole plant-world; yet it is possible that, as it is exhibited by the Compositæ in these islands, we may be in a better position to grapple with the problem. But before doing so it will be requisite to look a little closer at these early Hawaiian genera of the Compositæ.

The distribution within the archipelago of the genera and species of the early Compositæ of Hawaii is worthy of notice from the light it throws, not only on the relative antiquity of the genera, but also on the subsequent conditions of isolation. Of the nine genera here referred to five are distributed over most of the islands of the group. These include all the genera possessing a number of species, namely, Tetramolopium with seven species, Lipochæta with eleven, Campylotheca with twelve, Dubautia with six, and Raillardia with twelve species. Of the four genera remaining all have only two species, and are restricted to two or three islands, Remya and Wilkesia being in both cases found in Kauai and Maui, whilst Argyroxiphium is confined to the adjacent islands of Maui and Hawaii, and Hesperomannia to those of Oahu, Lanai, and Maui. These four genera that are restricted to only two or three islands are the same before referred to as regarded by Hillebrand as the oldest, partly on account of their isolated generic position, and partly because in each case they only possess two species.

Although the early Hawaiian Compositæ were evidently originally transported to most of the islands of the group, it is noteworthy that their subsequent isolation from the rest of the world has in the later ages been repeated within the limits of the archipelago. Of the 56 species, all of which are now endemic, 28, or just half, as shown in the table on the following page, are confined to a single island. Of the remainder, almost all are restricted to two or three adjacent islands. Hillebrand gives only a solitary species, Lipochæta connata, as occurring in all the islands. This suspension, to a great extent, of the means of dispersal between the islands is also strikingly illustrated by the Lobeliaceæ.

We have only to mention the flora of Fiji and those of the adjacent groups of Samoa and Tonga to exclude them from any share in the early era of the Compositæ in the Pacific. The prevailing adventitious character of the Fijian Compositæ is indicated in the fact that the species of the majority of the genera are included by Seemann in his list of Fijian weeds. There are only one or two Fijian Compositæ, such as the mountain species of Lagenophora and the littoral species of Wedelia, that merit the special attention of the student of dispersal. So also with Samoa, Reinecke enumerates eight species, of which six are weeds either of aboriginal or of European introduction, the others being the littoral Wedelia above alluded to, and a species of Blumea found also in Fiji.

DISTRIBUTION OF THE ENDEMIC GENERA OF COMPOSITÆ IN THE HAWAIIAN ISLANDS.

Genus.	Distribution of the Species.					Total.
	One island.	Two islands.	Three islands.	Four islands.	General.	
Remya	2	—	—	—	—	2
Tetramolopium	1	4	2	—	—	7
Lipochæta	3	4	3	—	1	11
Campylotheca	5	4	3	—	—	12
Argyroxiphium	1	1	—	—	—	2
Wilkesia	2	—	—	—	—	2
Dubautia	4	—	2	—	—	6
Raillardia	9	1	—	2	—	12
Hesperomannia	1	1	—	—	—	2
	28	15	10	2	1	56

We have now, I venture to think, gone far to establish the existence of an early "Composite" flora with mainly American affinities in the Pacific islands, an ancient flora of which only the remnants now occur in the uplands of Hawaii, Tahiti, and Rarotonga. That the achenes were originally transported in birds' plumage is, as we have seen, probable; but we are still quite in the dark as to the causes of the subsequent suspension of the means of dispersal and of the resulting period of isolation, during which the original immigrant plants acquired their endemic characters. In our uncertainty, therefore, we will look to Fiji in the hope that in the absence of the early Compositæ from that

group we may find a clue that will enable us to divest this problem of some of its difficulties.

It might be at first considered that since these peculiar genera of Compositæ occur in the higher levels of Hawaii and Tahiti their absence from Fiji might be connected with the relatively low altitude of those islands, a character that is concerned with the exclusion from the Fijian flora of many Hawaiian and Tahitian mountain plants (see Chapters XXIII. and XXIV.). But this view is at once negatived by the fact that Fitchia thrives in Rarotonga, an island which does not far exceed 2,000 feet in elevation. It is negatived also by the extensive development of shrubby and arborescent Compositæ in the Galapagos Islands, on the equator, in St. Helena in 16° South latitude, and in other tropical islands, which are less than, or do not exceed, the Fijian Islands in their altitude.

During the age of the Compositæ it is reasonable to suppose that the dispersal was general over the Pacific. The absence of genera indicating this era from the islands of the Fijian region, that is, from Fiji, Tonga, and Samoa, would become intelligible if these groups were submerged during this age of the general dispersal of the order over this ocean. In my volume on the geology of Vanua Levu in Fiji, I have shown that these island-groups of the Western Pacific emerged from the sea towards the close of the Tertiary period, a conclusion that would enable us to assign the age of the general dispersal of the Compositæ over the tropical Pacific to an earlier portion of the same period.

In order, however, to make further progress in the discussion of this difficult problem we are obliged to approach it from the outside. We must in fact regard these genera from the standpoint of their position as members of the vast and ancient order of the Compositæ. It is now more than thirty years since Mr. Bentham completed his remarkable memoir on the classification, history, and geographical distribution of the Compositæ (*Journal Linnean Society*, *Botany*, London, Vol. 13, 1873). Like De Candolle, when dealing with the facts of distribution, he handled thousands of species, and as a result he drew certain inferences which are of prime importance to students of plant-dispersal. In his time the order included nearly 10,000 known species, and although this number has since no doubt been considerably increased, it is not likely that his main conclusions, in so far as they are free from purely hypothetical considerations, will be materially affected by the later discoveries.

Accepting the antiquity of the order, and regarding it as probably dating far back in geological time, he observes that the evidence points to a very wide dispersion of its original stock at an early period. Africa, West America, and possibly Australia, possessed the order at the earliest recognisable stage. There must have existed, he contends, at this early period some means of reciprocal interchange of races between these regions. Then followed a stoppage of communication, or a suspension of the means of dispersal, between the tropical regions of the Old and New Worlds; but long after communication was broken off in the warmer regions, it still existed, as he holds, between the alpine heights in those regions and also between the high northern latitudes of both hemispheres. Referring particularly to the Hawaiian Group, he considers that the large endemic element among the Compositæ indicates that the ancient connection, whether with America or with Australasia, has been so long severed as not to have left a single unmodified common form. Fitchia, the Tahitian genus, as we have already remarked, is regarded as the only remnant of an ancient Composite flora in the tropical islands of the South Pacific.

In the light of these reflections it will be interesting to glance at the general distribution of the shrubby and arborescent or woody Compositæ. Mr. Hemsley, having generally discussed the subject, arrived at the conclusion that, "although they form so large a proportion of the floras of St. Helena, Juan Fernandez, the Sandwich Islands, and some other islands, they are not specially insular." There are scores of them, he goes on to say, in South America, Africa, Madagascar, India, Australia, and New Zealand from twenty to forty feet high, and more truly arboreous than the insular ones; whilst nearly every sub-order has its arboreous representatives. He was, however, unable to form any definite opinion of the method of distribution of the woody Compositæ. Taking those of St. Helena and Juan Fernandez, he observes that they are not more closely allied to the Compositæ of the nearest continents than they are to those of more distant regions. The occurrence of arboreous Compositæ, belonging in each case to different tribes, in so many remote oceanic islands, coupled with the distribution of the genera to which they bear the greatest affinity, seems, he observes, to indicate that they are the remains of very ancient types (*Introd. Bot. Chall. Exped.*, pp. 19—24, 66, 68; also Parts ii. p. 61, and iii. p. 23).

The further discussion of this subject would lead us into a wide

field of inquiry, quite beyond the scope of this work. There is, however, an inference that I think we may legitimately draw from geological evidence in this region. With respect to the antiquity of the woody Compositæ of the Pacific as illustrated by the endemic genera, both Mr. Bentham and Mr. Hemsley view them as belonging to ancient types. Mr. Wallace, in his *Island Life*, a book that becomes more and more indispensable for the student of dispersal as years progress, dwells on the importance of these ancient Compositæ in the floral history of the Pacific islands. We may look upon the Hawaiian Compositæ, he remarks, as representing the most ancient portion of the existing flora, carrying us back to a very remote period when the facilities for communication with America were greater than they are now. The date of this period of oceanic dispersal of the Compositæ we can now approximately determine, since these plants are absent from the Fijian region, an area of submergence during the Tertiary era. Before the island-groups of the Fijian region had emerged towards the close of the Tertiary period the achenes of the early Compositæ had been dispersed far and wide over the tropical Pacific.

But this is not all that we can infer from the convergence of these independent lines of botanical and geological investigation. Mr. Bentham observes that the tribes of the Compositæ had acquired the essential characters now employed in classification before the dispersion of the order over the Pacific. Since this general dispersion took place, as we hold, during the Tertiary submergence of the island-groups of West Polynesia (Fiji, Tonga, Samoa), it follows that the birth of the tribes of the Compositæ antedates that period. If this interesting order could supply us with a "datum-mark" in the history of the Pacific floras, it would be stated in terms of the development of specific and generic characters, but not of those of a tribe.

Summary of Chapter.

(1) The Hawaiian Islands present the same contrast with the Fijian and Tahitian groups as regards the development of new species in the case of the flowering plants that they offer in the case of the vascular cryptogams (ferns and lycopods). But the contrast is intensified, and it is further emphasised as respecting the flowering plants by the evolution of a large number of endemic genera.

(2) This great preponderance of peculiar species and genera in Hawaii is not to be connected with the relative antiquity of the group but with its degree of isolation.

(3) The earliest stage of the flowering plants of the islands of Hawaii and of Eastern Polynesia (the Tahitian region) is indicated by the endemic genera, particularly those of the Compositæ and Lobeliaceæ. Such genera are numerous in Hawaii, and occur also in the Tahitian region, as in Tahiti and Rarotonga; but do not exist in the groups of the Fijian region (Fiji, Tonga, and Samoa).

(4) The endemic genera of the Hawaiian Compositæ are mainly American in their affinities. The relationship of the solitary Tahitian genus (Fitchia) is still a subject of discussion.

(5) In the Hawaiian Islands, as well as in Tahiti and Rarotonga, the plants of the endemic genera of Compositæ are, as a rule, arborescent or shrubby; and in the first two localities they are mainly restricted to the higher levels.

(6) In discussing the mode of dispersal of the achenes of the original genera we have also to explain why the process of dispersal has been in the main suspended.

(7) It is shown that the achenes of these early Compositæ were in all probability suited for dispersal in birds' plumage.

(8) Yet the isolating influence that cut off these genera from the outside world has, in later ages, been active within the limits of the Hawaiian archipelago, with the result that half the species are not found in more than a single island. Inter-island dispersal has, therefore, been also largely suspended.

(9) The absence of endemic genera of Compositæ from Fiji, Tonga, and Samoa cannot be attributed to unsuitable climatic conditions connected with the relatively low elevation of those islands as contrasted with those of Hawaii, since a species of Fitchia abounds in Rarotonga, which is not far over 2,000 feet in elevation. Shrubby and arborescent Compositæ of peculiar types also occur in the Galapagos and other tropical islands not more elevated than the Fijis.

(10) These endemic genera are the remains of an ancient Composite flora in the islands of the tropical Pacific, and ages have elapsed since the severance of their connections with regions outside.

(11) According to Mr. Bentham the Compositæ were distributed over Africa, West America, and possibly Australia, at an early period, but subsequent to the differentiation of the tribes of

the order. Some means of reciprocal interchange of races between these regions then existed. Then followed a suspension of the means of dispersal between the tropical regions of the Old and New Worlds except between the alpine heights of those latitudes.

(12) It is inferred by the author of this volume that the general dispersion of the early Compositæ over the Pacific took place during the Tertiary submergence of the island-groups of the Fijian region (Fiji, Tonga, and Samoa), and that their absence from that region may be thus explained. At the time of this general dispersion, as above pointed out, the tribes of the Compositæ had been already differentiated.

CHAPTER XXII

THE ERA OF THE ENDEMIC GENERA (*continued*)

THE COMPOSITÆ AND LOBELIACEÆ (*continued*)

THE AGE OF THE TREE-LOBELIAS

The distribution of the arborescent Lobeliaceæ.—On the upper flanks of Ruwenzori.—The Lobeliaceæ of the Hawaiian Islands.—The Lobeliaceæ of the Tahitian or East Polynesian region.—The capacities for dispersal.—The explanation of the absence of the early Lobeliaceæ from West Polynesia.—The other Hawaiian endemic genera.—The Fijian endemic genera.—Summary.

THE Lobeliaceæ rank with the Compositæ in the prominence of their position in the early Pacific floras. Though absent, as far as is known, from Fiji, they are represented in Hawaii by 58 species, all endemic and belonging to six genera, of which five are not found elsewhere. All possess, as Hillebrand remarks, a woody stem, by far the greater number being either tall shrubs, 5 or 6 feet high, or small trees, 10 to 20 feet or more in height. In the East Polynesian or Tahitian region, the order is represented by two genera containing in all five known species and restricted to those islands. One genus is common to the islands of Tahiti and Rarotonga, and the other is confined to Raiatea. The species may be shrubby or arborescent.

It was for some time considered that the oceanic archipelagoes of the Pacific were the exclusive centres of these singular arborescent Lobeliaceæ (I am here quoting Baillon in his *Natural History of Plants*). And indeed this idea would receive some support from the circumstance that Dr. Hillebrand, in his work on Hawaii, says little or nothing about the affinities or general relations of plants which he enthusiastically termed "the pride of our flora." His death in 1886 deprived his work of its crowning piece, a discussion

of "the interesting questions of the origin and development of the Hawaiian flora" (see the Editor's Introduction, p. ix.). In no group of plants is this want more keenly felt than with the Lobeliaceæ. Yet in his time the explorations had yet to be made that could set the student of plant-distribution on the road to investigate this problem.

It was true, no doubt, that types analogous to those of the Hawaiian Lobeliaceæ were known from the American and African continents. Thus Oliver in his *Flora of Tropical Africa*, published in 1877, gives an account of the species of Lobelia then known from the mountains of this region. The genus was, however, not entirely confined to mountainous districts, but it would almost seem that most of the high mountains of Equatorial Africa had their peculiar species, some of them being tree-like and others shrubby. Two mountain species were recorded from Abyssinia, one of them from an elevation of 11,000 to 13,000 feet and growing to a height of 12 to 15 feet, the other from an altitude of about 8,000 feet; another, Lobelia Deckenii, attaining a height of 4 feet, was recorded from the uplands of Kilimanjaro, 12,000 to 13,000 feet above the sea, and yet another from the mountains of Fernando Po, at an altitude of 9,000 feet. So again, in the case of the American continent, Hemsley, writing in 1885 (*Intr. Bot. Chall. Exped.*, p. 32), speaks of arborescent species of the American genera Centropogon, Siphocampylus, &c.; and Baillon in his *Natural History of Plants* (Engl. edit. viii. 350) refers to the similar Tupas and Haynaldias from South America. But what the student of plant-distribution looked for was not merely the occurrence of "tree-lobelias" in other parts of the world, but also the reproduction of these wonderful plants under the same conditions and on the same scale as those familiar to him on the Hawaiian mountains. He has accordingly had to wait for the results of the more recent explorations of the mountains of Central Africa in order to obtain his wish.

On the upper flanks of Ruwenzori, Kilimanjaro, and Kenya, at elevations of 9,000 to 13,000 feet and reaching to the snow-line, there flourish in boggy portions of the forest arborescent Lobeliaceæ that attain a height of 15 or 20 feet. They have the habit sometimes of a Dracæna and sometimes of an Aloe, and do not exhibit the branching trunks so characteristic of the Hawaiian genus of Clermontia. They all belong, however, to the genus Lobelia, and thus do not display the extensive differentiation of the endemic genera of Hawaii. Nor, apparently, has there been the same

degree of formative energy in the development of species, since only about half a dozen species are hitherto known. We find, however, produced on these lofty mountains of Equatorial Africa the same climatic conditions under which the arborescent Lobeliaceæ flourish in Hawaii, namely, the very humid atmosphere, the heavy rainfall, and the mild temperature; and if there are important contrasts in their character and in the amount of differentiation which they have undergone in the two regions, the one a continental and the other an insular region, it will be from such contrasts that some of the most interesting results of this comparison of a mountain of Central Africa with an island of the open Pacific will be ultimately derived (see Sir H. Johnston's *Uganda Protectorate*, 1902, and *Kilimanjaro Expedition*, 1886; also *Trans. Linn. Soc. Bot.*, ser. 2, vol. 2, p. 341.

THE LOBELIACEÆ OF THE HAWAIIAN AND OF THE EAST POLYNESIAN OR TAHITIAN ISLANDS.*

HAWAIIAN ISLANDS.

Genus.	No. of species.	Distribution of genus.	Distribution in the group.	Height of plant.	Nature of station.	
					Elevation.	Station.
Brighamia ...	1	Endemic.	Molokai, Niihau.	5 to 12 feet.	Islands not exceeding 3,500 feet.	Steep palis or mountain gaps.
Lobelia	5	Non-endemic.	General.	4 to 6 feet.	2,000 to 6,000 feet.	Bridges, gulches and woods.
Clermontia ...	11	Endemic.	General.	Usually 10 to 20 feet.†	2,000 to 6,000 feet.	Open woods.
Rollandia	6	Endemic.	Oahu.	Usually 4 to 6 feet, one species 10 to 15 feet.	Higher parts of Oahu, which is 4,000 feet high.	Woods.
Delissea	7	Endemic.	General.	5 to 10 feet.	1,000 to 5,000 feet.	Woods and gulches.
Cyanea	28	Endemic.	General.	Usually 6 to 15 feet.‡	1,000 to 5,000 feet.	Woods, ravines, gulches.

EAST POLYNESIAN OR TAHITIAN ISLANDS.

Sclerotheca ...	4	Endemic in E. Polynesia.	Tahiti, Rarotonga.	6 to 25 feet.	1,500 to 3,000 feet.	Humid wooded slopes.
Apetahia	1	Endemic.	Raiatea.	3 to 6 feet.	In the mountains. Elevation of island 3,400 feet.	

* The materials are nearly all derived from the works of Hillebrand and Drake del Castillo. Some of those relating to the elevations in Hawaii are supplemented from my notes. All the genera are endemic except Lobelia, of which all the species are apparently endemic, excepting perhaps one, which, according to Hillebrand, resembles greatly a species from the Liukiu Islands.

† The range of the heights of different species of Clermontia is from 5 or 6 feet for shrubs to 25 feet for trees.

‡ The heights attained by different species of Cyanea range from 3 or 4 feet to between 30 and 40 feet, thus:—

In 8 species 3 to 6 feet.	In 3 species 15 to 25 feet.
" 9 " 6 " 10 "	" 1 " 30 " 40 "
" 7 " 10 " 15 "	

THE LOBELIACEÆ OF THE HAWAIIAN ISLANDS.

Having thus prepared the way, I will proceed to the discussion of the Hawaiian Lobeliaceæ, dealing first with their "station." Their vertical distribution is well illustrated in the large and lofty island of Hawaii. Whilst the woody Compositæ, as before described, are most at home on the open-wooded and often scantily-forested slopes between 5,000 and 9,000 feet, the Lobeliaceæ are most characteristic of the middle or true forest zone that extends from 2,000 or 3,000 feet to between 5,000 and 6,000 feet above the sea. This lies within the region of clouds and mists, and it is here that the rain-belt or area of greatest rainfall is situated, the annual amount averaging probably 150 to 200 inches. It is in such humid conditions that, as Hillebrand observes, trees and jungle are developed in greatest luxuriance; and it is here that "the Lobeliaceæ exhibit their most striking forms." The traveller, as he ascends the mountains, finds the Tree-Lobelias in the region of mist and rain-cloud; and he is lucky if he escapes the usual downpour and encounters only a fine drizzling rain.

The mild climate of this region is indicated by a mean annual temperature ranging probably with elevation from 65° to 55° F. It is secure from the frosts of the upper slopes of the mountain; whilst at the same time it is above the regions of tropical heat. There is, however, no doubt that when the forests extended to the coasts, as they occasionally do now on the north side of Hawaii, the Lobeliaceæ occurred much lower down than they do at present, though still only attaining their greatest development in size and number in the higher levels. Thus, at rare intervals, I noticed in the forests of Hamakua and Kohala, where they descended to the coasts, species of Clermontia at an elevation of only 500 or 600 feet above the sea.

Probably in no part of the Hawaiian Islands are the conditions under which the "Tree-Lobelias" thrive better illustrated than on the higher slopes of Mount Eeka, a bulky mountain mass about 6,000 feet in height, forming the western portion of Maui. Its flat top, as Hillebrand observes, is wrapped in a cloud of mist nearly the whole year. On the boggy surface of the summit, where Acæna exigua gives a tussocky appearance, and Sphagnum or bog-moss abounds, flourish Cyperaceæ, Lycopods, and Selaginellæ; and here Drosera longifolia and a peculiar species of marsh violet (Viola mauiensis) find a home. The upper slopes, down to 4,000 feet, present similar moist conditions, and here in an open-wooded

district, associated with Cyrtandræ, Marattias, and true Tree-Ferns, the ground being covered with Lycopods, the "Tree-Lobelias" abound. I noted four kinds within two hundred yards. Of the humidity of the upper slopes of Mount Eeka I have a very vivid recollection, and my experience of passing a night on that mountain is described in Chapter XIX.

The Lobeliaceæ, as Hillebrand remarks, occur invariably as isolated individuals. I was often struck, however, with the preference the genera showed for particular localities. Thus, Clermontia is well represented on the western slopes of Mount Eeka, Delissea on the northern slopes of Hualalai (3,800 to 4,500 feet), Cyanea on the Hamakua slopes of Mauna Kea (2,300 to 4,100), and Lobelia on the southern slopes of Mauna Loa behind Punaluu (2,000 to 3,500 feet).

To the student of geographical distribution the Hawaiian Lobeliaceæ are of especial interest. Mr. Hemsley observes that they have their greatest affinities in America (*Intr. Bot. Chall. Exped.*, p. 68). M. Drake del Castillo, in his "Mémoire couronné par l'Académie des Sciences" (Paris, 1890), remarks that these plants connect Hawaii with America just as the Goodeniaceæ link the same group with Australia. This is what we might have expected since the centre of the order is in America, principally in the Mexican and Andine regions (Drake del Castillo, *Flore Polyn. Franc.*, xi.).

Though five out of the six genera are endemic, the sixth, that of Lobelia, has a world-wide distribution. Here then, we have a genus that belongs strictly to the next or second stage of the plant-stocking of the Hawaiian Group, namely, when the non-endemic genera now containing endemic species were introduced. As with the Composite genera, Campylotheca and Lipochæta, Lobelia marks the beginning of the new or the close of the old era. It is, however, necessary to point out that many of the conditions favouring luxuriant and rank vegetable growth are pre-eminently represented in the zone of the Lobeliaceæ. In these soft-stemmed plants with their copious milky sap and large fleshy flowers, sometimes two or three inches long, the very redundancy of growth would tend both to exaggerate and to disguise the generic distinctions. To the ordinary observer these "Tree-Lobelias" call up vague notions of a flora of a bygone age, and by their *bizarre* appearance he might with some excuse be led to give play to his imagination when describing them; but the systematic botanist, seeing through their disguise, frames rather more prosaic notions of

their antiquity and degree of differentiation. According to my view, the first Hawaiian Lobeliaceæ occupied open, exposed localities such as are held by the decadent genus Brighamia now, and acquired their monstrous form in the humid forests of a later age. (See Perkins in Note 80.)

In his monograph on the Campanulaceæ (Engler's *Nat. Pflanz. Fam.*, teil 4, abth. 5, 1894), S. Schönland, speaking of the subfamily Lobelioideæ, places the seven endemic Hawaiian and Tahitian genera in a group by themselves. Though, as he observes, the Hawaiian tree-forms appear at first sight to constitute a natural group, they cannot be sharply distinguished from other forms, and even in habit come near some Indian and Abyssinian types of Lobelia. In their treatment, he says, they should all go together, and he does not approve of the endeavours of some botanists to isolate one of them (Brighamia) from the rest and to connect it with the Australian genus Isotoma.

It is also to be noted that whilst four of the Hawaiian genera are more or less dispersed over the group, one (Brighamia) with only one species is confined to the islands of Molokai and Niihau, the double habitat being suggestive of its approaching extinction. Another (Rollandia) with six species is restricted to the island Oahu. Cyanea, which possesses twenty-eight out of the total of fifty-eight species, may, from the point of view of its formative energy, be regarded as in its prime. It is thus apparent that, as with the Compositæ, the early Lobeliaceous immigrants were not all contemporaneous arrivals.

Another interesting fact of distribution, brought out by an analysis of Hillebrand's materials and illustrated in the subjoined table, is that out of the fifty-eight Hawaiian species, all of which are

DISTRIBUTION OF THE LOBELIACEÆ IN THE HAWAIIAN ISLANDS.*

Hawaiian Lobeliaceæ.	Brighamia.	Lobelia.	Clermontia.	Rollandia.	Delissea.	Cyanea.	Total.
Species confined to one island..	—	—	6	6	4	22	38
,, ,, two islands	1	2	2	—	2	5	12
,, ,, three ,,	—	1	2	—	1	1	5
Species generally distributed, but still endemic	—	2	1	—	—	—	3
	1	5	11	6	7	28	58

* All the species are endemic.

endemic, thirty-eight, or 66 per cent., are recorded from only one island. In most of the other cases they are recorded from two or

three islands, usually adjacent, like Maui and Molokai; and except in the instance of two species of Lobelia and one species of Clermontia they never range over the length of the group.

These facts speak eloquently of the suspension to a great extent of the agencies of dispersal in recent times within the group. Some corrections of the figures will be rendered necessary by future investigations, but the main conclusion will not be materially affected. Such facts are paralleled in the distribution of the Hawaiian insects, mollusca, &c.; but these matters need only be mentioned here. We might, indeed, have expected, apart from other considerations, that the isolation of the Hawaiian Lobeliaceæ from their kindred in other parts of the world would not have been reproduced within the group itself. This, however, is not the case; and we now see that not only have they been deprived for ages of their means of distribution over the Pacific, but that even within the archipelago their transportal from island to island has been largely suspended. We have before arrived at similar conclusions with regard to the early Compositæ, when we saw that about half the species were not found in more than one island. It is therefore evident that the same great principle regulating the operations of the distributing agencies has influenced to a similar extent both the Compositæ and the Lobeliaceæ of the Hawaiian Group.

THE LOBELIACEÆ OF THE TAHITIAN OR EAST POLYNESIAN REGION.

The order is represented in this region by two endemic genera, Sclerotheca of Tahiti and Rarotonga, and Apetahia of Raiatea. These islands are, however, not sufficiently large for the extensive development of the arborescent Lobeliaceæ, such as we find in Hawaii. The species in both genera are either arborescent or shrubby; but I do not gather that they give any character to the floras of these islands. According to the data given by Drake del Castillo for one of the two peculiar species of Sclerotheca occurring in Tahiti, these plants grow on the humid wooded slopes of the mountains at elevations of 2,000 to 3,000 feet. Whilst in one species the plants attain a height of 10 to 25 feet, in the other they do not exceed 10 feet. Rarotonga possesses a peculiar species of Sclerotheca, 4 to 6 feet high, which was discovered by Cheeseman growing plentifully on the upper slopes of the highest mountain of the island at altitudes of 1,500 to 2,200 feet. The same botanist also came upon a second species of the genus on another mountain

in Rarotonga at elevations of 1,000 to 1,500 feet, but it was rare and has not yet been described. The other genus, Apetahia, has only been recorded from Raiatea, where it is represented by a solitary species (6 feet high) growing, according to Nadeaud, in the mountains of that island.

It is apparent that the dispersal of these genera of the Lobeliaceæ amongst the groups of Eastern Polynesia ceased long ago. From the circumstance that Sclerotheca exists in Tahiti and in Rarotonga, which are about 650 miles apart, it may be inferred either that the genus was introduced into this region from outside, or else, which is perhaps more probable, that it was developed in Tahiti whence it was transported to Rarotonga. Hemsley speaks of this Tahitian genus as seemingly marking a former wide extension of the Hawaiian arborescent type of the Lobeliaceæ (*Introd. Bot. Chall. Exped.*, p. 68). This is the view that will be adopted in this chapter, and it is precisely the view advocated by Bentham and followed here, in the case of the early Compositæ of the Pacific.

With regard to the absence of these arborescent Lobeliaceæ from the island-groups of the Western Pacific, and notably from Fiji and Samoa, where no members of the order seem to occur, it is probable that, as in the case of the similar distribution of the early Compositæ described in the preceding chapter, this is to be attributed to the fact that the Western Pacific archipelagoes were more or less submerged during the general dispersion of the Compositæ and Lobeliaceæ over the Pacific in the earliest age of the floral history of these islands. The occurrence of the early Compositæ and Lobeliaceæ in Rarotonga, which is almost halfway between Tahiti and Tonga on the outskirts of the Fijian region, sufficiently indicates that they are not lacking in that region from inability to reach there in the past. During the age of general dispersal of these two orders over the Pacific, probably only a few rocky islets, tenanted perhaps by Conifers, marked the situation in the Tertiary period of the present archipelagoes of Fiji and Samoa.

One may note in passing the general absence of these arborescent types of the Lobeliaceæ from Malaya, since they do not seem to have been recorded either from the Owen Stanley Range in New Guinea or from Kinabalu in North Borneo, the highest mountain in the Malayan Islands, or from the mountains of Java.

The consideration of the occurrence of these plants in other tropical or subtropical oceanic islands need not detain us long,

since, with the exception of the solitary Lobelia scævolifolia of St. Helena, they seem rarely to be found. This species, which is endemic, is a shrub growing on the upper slopes and summit of the island at elevations of 2,000 to 2,700 feet (*Introd. Bot. Chall. Exped.*, p. 40, and Part ii. pp. 54, 76).

There are two herbaceous species of Lobelia in Juan Fernandez, of which one only, according to Hemsley, could be regarded as indigenous. This is a showy Chilian and Peruvian species (Lobelia tupa) noticed by Bertero as very common in 1829 (*Bot. Chall. Exped.*, Part iii.). Since, however, it would belong to the present age of plant-dispersal in the Pacific, it does not require further mention here; and indeed it would almost appear, when we bear in mind the geographical position and the history of this island since its discovery in 1563, that even as a truly indigenous plant it is not above suspicion. Lobelias of this type are now amongst the commonest plants of the coast regions of northern Chile, where I noticed some as much as 9 or 10 feet high.

On the Capacities of Dispersal of the Lobeliaceæ of the Pacific.—Of actual observations, with the exception of the instance of birds pecking at the capsules of our garden Lobelias, I have come upon few that bear directly on this point. When writing of the flora of the Kermadec Group, many years ago, Sir Joseph Hooker referred (*Journ. Linn. Soc. Bot.*, vol. i.) to the minute seeds of Lobelia as not adapted for transport unless their minuteness and number fit them for it; but since he associates in this connection the tiny seeds of Metrosideros, which is now represented by a species found all over the Pacific, it would seem that the difficulty in the case of Lobelia is not connected so much with the nature as with the suspension of these means of distribution during the later stages of the plant-stocking of the oceanic islands of the tropical Pacific. It will be gathered from the following remarks that the descendants of the early Pacific Lobeliaceæ are probably as well fitted for dispersal as their ancestors, and that the break in the communication is the ultimate subject for inquiry.

The fruits of the Hawaiian endemic genera are in four out of five cases baccate, with usually fleshy or pulpy contents. Such berries, which are generally yellow, but sometimes bluish in colour, vary in size from about half an inch in Rollandia and Delissea to an inch in Cyanea, and not infrequently to more than an inch in Clermontia. The fruits of Lobelia and Brighamia are capsular and dehiscent. With regard to the two genera of the Society Islands and Rarotonga, the fruits of Sclerotheca are hard-walled

capsules, opening by two pores; whilst those of Apetahia are seemingly dry and indehiscent. I do not imagine, therefore, that the character of the fruit has determined to any important degree the distribution of these plants.

Nor is there reason to suppose that the fruits have acquired their baccate character in Hawaii, and that they were originally dry and capsular. Both types of fruit are found among the arborescent Lobeliaceæ of America, with which the Hawaiian genera have their affinities. Centropogon, for instance, which occurs in Central America and in the warm parts of North and South America, has, according to Baillon, a somewhat fleshy berry. It is noteworthy that a similar question is raised with respect to Cyrtandra as to the relation between fleshy fruits in the Pacific islands and dry or capsular fruits in the continental home of the genus (see Chapter XXV.).

The berries of the Tree-Lobelias would attract birds. We learn from Mr. Perkins that one of the Hawaiian Drepanids, the Ou, is very partial to the berries of some of the Tree-Lobelias and especially those of Clermontia, the seeds passing unharmed in the droppings. The mode of dispersal of the seeds of the dry-capsular fruits is not so apparent; but the fruits could scarcely be less inviting to birds than the dry capsules of Metrosideros, the small seeds of which have in some way or other been carried to almost every island-group of the Pacific. I have beside me the dark brown, smooth crustaceous seeds of a species of Clermontia. They measure $\frac{1}{42}$ of an inch or 0·6 of a millimetre, and about 500 go to a grain. Mr. Wallace, in his book on Darwinism, advocates the paramount influence of winds over birds for carrying small seeds, like those of Orchis and Sagina, over tracts of ocean a thousand miles across. I am, however, not inclined to think that, except as regards the spores of cryptogams, winds have done very much for Hawaii. For small seeds we can appeal not only to the agency of birds and bats but also to insects (see Chapter XXXIII.).

Observations of this kind, however, merely indicate that these early Lobeliaceæ possessed the same capacities for dispersal that in the succeeding stages of the plant-stocking of the Pacific islands have belonged to Metrosideros, Cyrtandra, Ophiorrhiza, Freycinetia, and many other small-seeded genera. They go no way to explain why the same agencies which transported the minute seeds in a later age could not have been available for continuing the dispersal of the early Lobeliaceæ. To find an explanation we are compelled

to go behind the mere capacities for dispersal and to appeal to the general laws of distribution in so far as our facts enable us to interpret them.

We have seen that the two principal components of the early Pacific flora, the Compositæ and the Lobeliaceæ, have American affinities. The plants of the later ages are mainly Old World in their connections. Though containing often endemic species in the various groups, the genera occur also outside each group. The stream of migration that came from America during the early age of the Compositæ and the Lobeliaceæ, when the islands of the Western Pacific were more or less submerged, was during the later ages (after these islands had re-emerged) suspended or diverted, giving place to a stream that brought plants in numbers from tropical Asia, Malaya, and Australia. The general dispersion of the Compositæ and Lobeliaceæ took place during the Tertiary submergence of the islands of the Western Pacific, including the island-groups of Fiji, Samoa, and Tonga. The migration from the west, mainly Indo-Malayan in character, occurred after the re-emergence of those archipelagoes. Thus we get to understand how genera like those of the early Lobeliaceæ and Cyrtandra, which possess, as regards the minute size of their seeds, closely similar capacities for dispersal, have such different distributions, the first confined to Hawaii and Tahiti and American in their affinities, the second widely spread over the Pacific with its home in Malaya.

We have yet to inquire whether this suspension of the means of transport in the later ages of the Pacific Lobeliaceæ is confined to the tropics or whether it extends to the colder latitudes in the southern hemisphere. The indications of the Lobeliaceæ of the "antarctic flora" go to establish that the dispersal of the order is still, or was very recently, in operation in these high latitudes. It is well illustrated, among other plants, by Lobelia anceps, which is found in extra-tropical South America, Australia and New Zealand, and South Africa. This, indeed, recalls Bentham's view concerning the Compositæ, that whilst communication was broken off in the tropics, it was kept up in higher latitudes.

Here ends, therefore, our consideration of the Tree-Lobelias of the Pacific islands; but as it is not quite complete without a discussion of the remaining endemic genera of other orders than the Compositæ and Lobeliaceæ which also belong to the same early age of the Pacific floras, I will proceed at once to their consideration.

THE HAWAIIAN ENDEMIC GENERA EXCEPTING THOSE OF THE COMPOSITÆ AND LOBELIACEÆ.

It will not be possible for me to do more than point out a few general indications that can legitimately be drawn from these genera. The subject bristles with difficulties for the systematist; but on one point there can be but little danger of going astray, namely, in imputing to them a high antiquity in the floral history of Hawaii. This can be said of all of them, whether or not the generic distinction adopted in Dr. Hillebrand's work is always adopted by botanists. It is therefore in this general sense that they may be regarded as belonging to the early age of the Hawaiian flora.

Although the genera of Compositæ and Lobeliaceæ are prominent amongst the representatives of the original flora of the Hawaiian Islands, forming about two-fifths of the whole, the genera of other orders are by no means inconspicuous, and their variety is shown in the fact that though twenty-three in number they belong to twelve orders. It is possible to divide these genera into two groups—one the older and perhaps more or less contemporaneous with the Lobeliaceæ and Compositæ, the affinities when apparent being American; the other the more recent and marking the close of the first era of the plant-stocking of these islands, the affinities being all with the Old World, and especially with Malaysia. This grouping is indicated in the list subjoined; and it may be here remarked that whilst shrubs, undershrubs, and perennial herbs of the Caryophyllaceæ, Labiatæ, and Urticaceæ form the features of the earlier group, trees of the Rubiaceæ and Araliaceæ are the most conspicuous members of the later group. At the close of the earliest era known to us of the floral history of the Hawaiian Islands we observe the commencement of those forests that now throughout Polynesia as well as in Hawaii betray their Asiatic origin.

In making this distinction I am proceeding on the assumption that the stream of migration, at first chiefly American in its source, came ultimately in the main from the Asiatic side of the Pacific. The change commenced, as I hold, in the latter portion of the first era of plant-stocking, an era characterised by the arrival of those early plants that are now represented by the endemic genera of the archipelago. The genera of this early period that belong neither to the Compositæ nor to the Lobeliaceæ are, as above observed, arranged by me in two groups, one regarded as

contemporaneous with, the other as of later origin than, the genera of these two orders. To the first belong the shrubby, highly differentiated genera of the Caryophyllaceæ, Schiedea and Alsinidendron, and the Labiate genera, similarly differentiated, of Phyllostegia and Stenogyne. To the second belong the Rubiaceous genera Kadua, Gouldia, Bobea, and Straussia, the Araliads Cheirodendron, Pterotropia, and Triplasandra, and the Loganiaceous Labordea.

In the earlier group the fruits are dry in half the genera, and in such cases granivorous birds probably were usually the transporting agents. Only in one case (Nothocestrum) is the fruit a berry, and in the other cases we have fruits like the fleshy nucules of Phyllostegia and Stenogyne which would probably attract birds. In the later group two-thirds or three-fourths of the genera have moist fruits such as would be eaten by frugivorous birds. Of these most are drupes, possessing not a single stone, but two or more pyrenes. This is the first appearance of the drupe in the plant-history of the archipelago. The Rubiaceous type of drupe inclosing two or more pyrenes plays a very conspicuous part in the distribution of plants over the Pacific in the succeeding eras.

I would here lay stress on an important characteristic of all the fruits of the endemic genera of the Hawaiian Islands. There are no "impossible" fruits of this era in Hawaii, such as we occasionally find in the succeeding eras. I mean by this term, fruits that defy the efforts of the student of distribution to explain their transport in their present condition. The discovery of a new inland genus possessing dry indehiscent fruits three or four inches long, or even of a single species of the coniferous Dammara, would play havoc with all our views respecting the stocking of these islands with their plants. The finding here of a large marsupial would scarcely produce more astonishment. The fruits indeed of this early era are very modest in their size, the dry indehiscent fruits and the stone-fruits rarely exceeding half an inch (12 mm.) in size.

There is another interesting point which is connected with the deterioration of some of the fruits in their capacity for dispersal. Some of the species of Phyllostegia, and a few also of the Araliads, as well as those of Nototrichium, are ill fitted for dispersal by birds now, the coverings of the seeds being not sufficiently hard to protect them from injury in a bird's stomach. At the same time there are in some cases other species of the same genera that are better suited for this mode of transport. The effect of dispersal

by frugivorous birds is that only the hard-coated seeds propagate the plant in a new locality. When, however, as has occurred in the Hawaiian Islands, bird-agency largely ceases to act, this selective influence is removed (see Note 68).

ENDEMIC HAWAIIAN GENERA, EXCLUDING THOSE OF THE COMPOSITÆ AND LOBELIACEÆ, AS GIVEN IN HILLEBRAND'S "FLORA OF THE HAWAIIAN ISLANDS.'

[Those preceded by * are not usually regarded now by botanists as endemic, though they nearly take that rank.]

THE EARLIER GROUP.

Genus.	Order.	Number of species.	Character.	Fruit.	Affinities.
Isodendrion......	Violaceæ.	3	Shrubs.	Capsule.	American (H).
Schiedea	Caryophyllaceæ.	17	Undershrubs, &c.	Capsule.	Near Colobanthus of the Antarctic islands, temperate South America, and Australia (C).
Alsinidendron...	,,	1	Undershrubs.	Capsule, with fleshy calyx.	
Platydesma......	Rutaceæ.	4	Small trees or shrubs.	Capsule.	—
Hillebrandia ...	Begoniaceæ.	1	Herbs.	Capsule.	—
Nothocestrum..	Solanaceæ.	4	Small trees.	Berry.	South American (H).
*Haplostachys ..	Labiatæ.	3	Herbs.	Dry nucules.	Regarded by Gray as a section of Phyllostegia.
*Phyllostegia ...	,,	16	Undershrubs.	Fleshy nucules.	Belong to the tribe Prasiæ, which is mostly Asiatic. Two other species of Phyllostegia recorded from Tahiti and Paumotu Islands.
Stenogyne	,,	17	Trailers or climbers.	Fleshy nucules.	
Charpentiera ...	Amarantaceæ.	2	Trees.	Utricle.	American (H).
Touchardia	Urticaceæ.	1	Shrubs.	Achene with fleshy perigone.	—
Neraudia	,,	2	Shrubs.	Achene with fleshy perigone.	Allied to Bœhmeria, a genus of Old and New Worlds.

THE LATER GROUP.

Genus.	Order.	Number of species.	Character.	Fruit.	Affinities.
*Pelea	Rutaceæ.	20	Trees.	Capsular.	Belongs to Melicope, an Old World genus (IK).
Broussaisia	Saxifragaceæ.	2	Small trees.	Berry.	Malayan (H).
*Cheirodendron..	Araliaceæ.	2	Trees.	Drupe.	Referred to Panax, an Old World genus (IK).
*Pterotropia	,,	3	Trees.	Drupe.	Malayan (H). Pterotropia referred to Heptapleurum of Old World (IK).
Triplasandra ...	,,	4	Trees or shrubs.	Drupe.	
Kadua	Rubiaceæ.	16	Shrubs, &c.	Capsular	Approaches both Asiatic and American types (C).
Gouldia	,,	5	Small trees or shrubs.	Drupaceous berry.	American (C).
*Bobea	,,	5	Small trees.	Drupe.	Malayan (H). Genus also in Malaya (IK).
Straussia	,,	5	Trees.	Drupe.	Near Psychotria, a genus of Asia and America (H).
Labordea	Loganiaceæ.	9	Small trees or shrubs.	Capsule with pulp.	Malayan (H).
*Nototrichium ..	Amarantaceæ.	3	Trees or shrubs.	Utricle.	Referred to the Australian Ptilotus (IK).

(H) = Hillebrand's *Flora of the Hawaiian Islands.*
(C) = Drake del Castillo's *Remarques sur la Flore de la Polynésie.*
(IK) = *Index Kewensis.*

NOTE.—Probably Schumann's genus, Pteralyxia, should be placed in the later group (see p. 154).

Another feature of interest is to be found in the distribution within the archipelago of the species of the peculiar genera. As in the case of the Compositæ and Lobeliaceæ, but few of the species are generally distributed, most being restricted to one island or to two or three adjacent islands. The suspension of the dispersal among the islands is, however, not so marked as with the species of the two orders just named.

NOTE.—Some further remarks on some of these genera are given in Note 68.

THE ENDEMIC GENERA OF THE FIJIAN ISLANDS.

The interest that is associated with the endemic genera of Hawaii fails to attach itself to those of Fiji. For this there are several reasons. In the first place, our acquaintance with the Fijian flora is much less complete. In the next place, the group holds a much less isolated position, and the history of an endemic genus may have a significance quite different from that connected with it in Hawaii. Fiji also lacks, on account of its submergence in the Tertiary period, those highly interesting genera of the Compositæ and Lobeliaceæ that form the chief feature in the early history of the flowering plants of Hawaii. Then, again, on account of our imperfect knowledge of the floras of the neighbouring groups of continental islands to the westward, the New Hebrides, Santa Cruz, and Solomon Groups, we can never feel quite confident that any particular genus is really peculiar to the Fijian archipelago. This is well brought out in the later history of the genera designated by Dr. Seemann in his *Flora Vitiensis* as peculiar to Fiji.

Of the sixteen genera enumerated by Dr. Seemann, and given in the table below, only about half now retain their character of being restricted to Fiji. Nor does it seem likely that future investigations will increase this number, since, judging from a remark made by Mr. Hemsley in his paper on the botany of the Tongan Group, explorations subsequent to those of Dr. Seemann, more especially those of Mr. Horne, have not apparently added a single new endemic genus to the Fijian flora. It will be seen from the list that at least four of the sixteen genera have since been found in the Malayan region, and in one case (Smythea pacifica) the same species occurs in both regions; whilst a fifth genus (Haplopetalon) has been recorded from New Caledonia.

There are, however, some peculiarities about the Fijian endemic genera that will attract our attention from the standpoint of dispersal. One remarkable feature is the paucity of species. Almost all the genera are monotypic, that is to say, they are only known by a single species. Amongst the twenty-eight Hawaiian genera that are strictly endemic, only four or five are monotypic, and they are mostly regarded by Hillebrand as worn-out, decadent types found in only one or two islands. In Hawaii there are on the average six species to each endemic genus; and it is thus apparent that in the display of formative energy Nature has worked on very different lines in these two groups. Since the nine Fijian endemic genera belong to nearly as many different orders, the composition of this endemic generic flora is by no means homogeneous. It is, I venture to think, such a motley collection as one might expect in a region that has been exposed to wave after wave of migration from the west, with no lofty mountains, as in Hawaii, to afford a refuge against extinction. It by no means follows that all these endemic genera have been produced in Fiji. Some of them may represent genera that have become extinct in the large continental groups to the westward.

SEEMANN'S SIXTEEN FIJIAN ENDEMIC GENERA.

Genus.	Order.	Number of species.	Character.	Fruit.	Affinities or other localities.
Richella	Anonaceæ.	1	Tree.	Baccate (?).	Indian in type (C).
Trimenia	Ternstrœmiaceæ	1	Tree.	Unknown.	
Pimia	Sterculiaceæ.	1	Tree.	Small spinose capsule.	Related to Australian genera (S).
Græffea	Tiliaceæ.	1	Tree.	Unknown.	Near Trichospermum, a Fijian and Malayan genus (S).
Thacombauia	Humiriaceæ.	1	Shrub.	Drupe.	Order mainly South American.
Amarouria	Simarubeæ.	1	Tree.	Dry drupe.	Near Soulamea, a Malayan genus (S).
*Smythea	Rhamneæ.	1	Straggling shrub.	Capsule.	Also in Burma, New Guinea, and Malaya (IK), (Sc).
*Oncocarpus	Anacardiaceæ.	2 (H)	Tree.	Drupe.	Also in New Guinea (IK).
*Haplopetalon	Rhizophoreæ.	2	Shrub.	Unknown.	Also in New Caledonia (IK).
*Nesopanax	Plerandreæ.	1	Tree.	Drupe.	=Plerandra (IK).
Bakeria	Plerandreæ.	1	Tree.	Drupe.	
Pelagodendron	Rubiaceæ.	1	Shrub.	Berry.	
*Paphia	Ericaceæ.	1	Shrub.	Berry.	=Agapetes, a Malayan genus (IK).
*Carruthersia	Apocyneæ.	2 (H)	Climber.	Berry.	Also in Philippines (IK).
*Couthovia	Loganiaceæ.	2	Tree.	Drupe.	Also in Kaiser Wilhelmsland, New Guinea (So).
Canthiopsis	Loganiaceæ.	1	Shrub.	Drupe.	

Those genera marked * have since been found outside the group.
The authorities are thus indicated: (C)=Drake del Castillo; (H)=Horne; (IK)=*Index Kewensis* (S)=Seemann; (Sc)=Schimper; (So)=Solereder in Engler's *Nat. Pflanz. Fam.*

The fact that several of them are fitted for dispersal by frugivorous birds is very suggestive of the lack of means of transport in later times. In the instance of Couthovia corynocarpa the drupes are known to be the food of fruit-pigeons at the present time (Seemann), whilst this is also true of Oncocarpus vitiensis, though this genus has since been found in New Guinea. Since, as will be pointed out in a later chapter, birds must still be fairly active in carrying seeds to Fiji from regions westward, it would seem that genera only become peculiar to Fiji when they fail at their source, and it is indeed doubtfu whether any of the Fijian peculiar genera are home productions. One may instance in this connection the genus Pimia, the fruits of which are especially well suited for attachment to a bird's plumage, yet it is only known from Fiji.

It should be here observed that no peculiar generic types have been recorded from the adjacent Tongan Group, and scarcely any from Samoa. Except perhaps with the Palmaceæ, no peculiar genera seem to be mentioned in Dr. Reinecke's memoir on Samoa.

Summary.

(1) The Lobeliaceæ, like the Compositæ, take a prominent place in the early Pacific flora, being represented, more particularly in Hawaii but also in the East Polynesian or Tahitian region, by endemic genera of tall shrubby and tree-like species.

(2) Tree-Lobelias occur in other parts of the world, as in South America and tropical Africa; but it is especially on the higher slopes of the mountains of Equatorial Africa that they attain a development comparable with that of Hawaii.

(3) In Hawaii the Tree-Lobelias are most characteristic of the middle forest-zone (3,000–6,000 feet), where the temperature is mild, the rainfall heavy, and the atmosphere laden with humidity.

(4) The affinities of these endemic genera of the Lobeliaceæ are mainly American; but their generic distinctions have been both exaggerated and disguised by redundant growth.

(5) From the distribution of the genera and species within the Hawaiian Group it is evident that, as with the early Compositæ, the original Lobeliaceous immigrants were not all contemporaneous arrivals. Some of the genera are on the point of extinction, whilst others are in their prime.

(6) The absence of the Lobeliaceæ from the groups of the Fijian area (Fiji, Tonga, Samoa) is probably to be connected, as in

the case of the absence of the early Compositæ, with the circumstance that the general distribution of these two orders over the tropical Pacific occurred during the Tertiary submergence of these archipelagoes.

(7) These endemic genera of the Lobeliaceæ possess the same facilities for dispersal that are owned by other genera with minute seeds, such as Cyrtandra, &c., that are dispersed over the Pacific; but in the case of the Lobeliaceæ the agencies of dispersal have been for ages suspended.

(8) This suspension is to be associated with the diverting of the main stream of migration from its source in America, during the early age of the Lobeliaceæ and Compositæ, to a source on the Asiatic side of the Pacific.

(9) The Hawaiian endemic genera other than those of the Compositæ and Lobeliaceæ arrange themselves in two groups—an earlier group containing highly differentiated Caryophyllaceæ and Labiatæ, and belonging to the age of the Compositæ and Lobeliaceæ; and a later group, characterised by Rubiaceæ and Araliaceæ, which marks the close of the first era, as well as the change in the main source of the plants from America to the Old World, the beginning of the Hawaiian forests, the appearance of the Rubiaceous drupe, and the first active intervention of frugivorous birds.

(10) Though there are no "difficult" or "impossible" fruits (fruits, the dispersal of which is not easy to explain) amongst the forty and odd endemic genera of Hawaii and Tahiti, it is noteworthy that in some cases the fruits are seemingly little fitted for dispersal now, and that this deterioration in capacity for dispersal is to be frequently associated with more or less failure of the inter-island dispersal in the case of Hawaii.

(11) The interest associated with the Hawaiian endemic genera fails to attach itself to those of Fiji, where genera only seem to have become peculiar because they have failed at their sources in the regions to the west. The endemic genera of the Compositæ and Lobeliaceæ are here lacking, and this is true also of the neighbouring Samoan and Tongan Groups, it being held that the age of the general dispersion of these orders over the Pacific corresponded with the Tertiary submergence of the archipelagoes of the Western Pacific. Those of Fiji, which do not amount to ten in number, belong to nearly as many orders and present a motley collection such as one might look for in a group much less isolated than Hawaii and exposed to wave after wave of migration from the west.

CHAPTER XXIII

THE ERA OF THE NON-ENDEMIC GENERA OF FLOWERING PLANTS

THE MOUNTAIN-FLORAS OF THE PACIFIC ISLANDS AS ILLUSTRATED BY THE NON-ENDEMIC GENERA

The mountain-flora of Hawaii.—A third of it derived from high southern latitudes.—An American element.—Compared with Tahiti and Fiji.—Capacities for dispersal of the genera possessing only endemic species.—Acæna, Lagenophora, Plantago, Artemisia, Silene, Vaccinium, &c.—Capacities for dispersal of the genera possessing non-endemic species.—Cyathodes, Santalum, Carex, Rhynchospora.—Fragaria chilensis, Drosera longifolia, Nertera depressa, Luzula campestris.—Summary.

THE AGE OF THE ENDEMIC GENERA OF FLOWERING PLANTS.

WE are now entering an era distinguished from the preceding age of the endemic genera, the age chiefly of the Compositæ and Lobeliaceæ, by the fact that the extreme isolation that followed that era no longer prevails. In a sense these island-floras are in touch again with the world around, though the main stream of plant-migration now comes from the south and from the west. Yet in a large number of cases, the amount varying greatly in the different groups, it is evident that this stream has not flowed continuously to the present day. The agencies of dispersal are often no longer active; but the period of inactivity has not been sufficiently prolonged to produce generic distinction, and the differentiating energy has been restricted to the development of new species.

Yet within these limits the development of new forms, as indicated in Table B on p. 233, has often been very great. Thus, nearly half the Hawaiian genera that are non-endemic are composed entirely of species not found outside the group; and in

this sense they may be regarded as cut off from the regions around. In Fiji and Tahiti only about a fourth are in this manner isolated, the agencies of dispersal being still effective with the majority of the genera. It is apparent, therefore, that the same question concerning the cause of the failure of the means of dispersal presents itself in this era as in the last, and most markedly in the instance of Hawaii.

The simplest and quickest plan for bringing into relief the prominent features of this age is first to regard the genera from the standpoint of the elevation of their stations. We have before remarked that in the occurrence of extensive regions of great altitude the Hawaiian Islands differ conspicuously from the groups of Tahiti and Fiji (and I may add Samoa); and that they present conditions for the development of a temperate mountain-flora that are not found at all in Fiji and are barely represented in Tahiti. That the Hawaiian flora responds to this contrast between the elevations of the three groups is well established; and I will now proceed to refer more in detail to the subject.

THE MOUNTAIN-FLORAS OF THE PACIFIC ISLANDS.

In the Hawaiian Islands there are at least 37 or 38 genera, making up about 19 or 20 per cent. of those belonging to this era, that may be designated mountain genera, nearly all of them being characterised as appertaining exclusively or in the main to temperate regions, or as frequenting mountain-tops in tropical latitudes. In Tahiti there are only 7 or 8 of such genera, about 4 per cent. of the total for the era. In Fiji, excluding the Conifers, there are only 4 or 5, or not 2 per cent. of the whole. In Samoa, which may be included in the Fijian area, there are 3, or about 2 per cent. of the total. These are results which we might have expected from the varying altitudes of these groups, as described in Chapter XIX.

Few things give more pleasure to the botanist than his recognition in some remote locality of plants long familiar to him in other regions. This will often be his lot on the mountain summits of Hawaii. If he has been a mountain-climber in many countries, he will there notice again the genera Artemisia, Geranium, Plantago, Ranunculus, Rubus, Sanicula, Vaccinium, and others that he has met perhaps either in the Rocky Mountains or in the Andes or in Equatorial Africa or in the Himalayas. If fresh from Chile he will find on these heights the familiar Gunnera

and the Chilian Strawberry (Fragaria chilensis). If he has been in New Zealand and in the islands of the Southern Ocean he will find old friends in the genera Acæna and Coprosma. He may handle once again plants like Nertera depressa, that he gathered on Tristan da Cunha; and on the boggy summits of some of the mountains he will find the ubiquitous Sun-dew (Drosera longifolia).

Within the limited area occupied by the peaks of Tahiti he will find genera like Astelia and Coprosma that are at home in New Zealand or in Antarctic America, and may even find, as in the cases of Coriaria ruscifolia and Nertera depressa, the identical species that are at home in those distant regions. Even on the summit of Rarotonga he will gather a species of Vaccinium. In Fiji, here and there on some isolated mountain-top he may come upon a remnant of this Antarctic flora, such as a solitary species of Coprosma or Lagenophora, that will carry him back for a moment to high southern latitudes; and in the highlands of Savaii, in the neighbouring Samoan Group, he will find again Nertera depressa and a species of Vaccinium. But that which will interest him most in Fiji will be the tall conifers of the genera Dammara, Podocarpus, and Dacrydium, which will bring to him memories perhaps of New Zealand and southern Chile, of South Africa, and of the mountain-woods of Java and of Southern Japan.

Yet the influence of isolation has been at work amongst the mountain-plants of all these groups. The agencies that have dispersed over the tropical Pacific plants from the cold latitudes of the southern hemisphere, and those that have borne the seeds of Plantago, Sanicula, and Vaccinium from mountain-top to mountain-top, even though it be to a peak in mid-ocean, are to a great extent inactive now.

The Mountain-Flora of Hawaii as illustrated by the Non-endemic Genera.

Let us look in the first place at Hawaii, where the breaking off of communication with the outside world is especially pronounced. Here, all the species of two-thirds or more of the mountain-genera are confined to that group. Only in a relatively small number of cases are the species in touch with the regions outside. The mystery of disconnection that is so evident in the instance of the peculiar or endemic mountain-genera of the Compositæ and Lobeliaceæ and other orders is here again presented to us, and

once more in the upland regions 4,000 to 10,000 feet above the sea. We will now endeavour to discover from an examination of the present distribution of the isolated mountain-genera (those non-endemic genera possessing only peculiar species) along what tracks they arrived at the Hawaiian uplands, tracks, as indicated by the local distribution of the species, that have been more or less abandoned since.

The Mountain Genera with only Endemic Species.—By referring to the Table on the following page it will be observed that nearly a third of these mountain genera have now their principal homes in the high latitudes of the southern hemisphere. They are components of what Forster and Hooker have termed the "Antarctic" flora, a collection of plants that range round the globe in high southern latitudes, namely, over Fuegia, New Zealand, southern Australia, South Africa, and the islands of the Southern Ocean, the "Antarctic" islands, as they have been termed. These genera are Acæna, Gunnera, Coprosma, Lagenophora, Astelia, Oreobolus, and Uncinia. (It is necessary to observe that I am entirely indebted to the Introduction to the *Botany of the "Challenger" Expedition* for my information on the "Antarctic" flora.)

We are thus led to expect that some of the other mountain genera may have been similarly derived from cool southern latitudes, even though they may be scarcely included in the "Antarctic" flora. This is very probably true of Myoporum and Exocarpus, two genera that are chiefly centred in Australia. A species of Sophora (S. tetraptera) is now one of the most widely dispersed of the plants of high southern latitudes, a circumstance which at all events explains the capacity for transport that the ancestor of the Hawaiian "Mamani" (S. chrysophylla) must have originally possessed (see Chapter XV.). Kinship between the Hawaiian species and southern forms has been found in the case of a few of the widely ranging genera here represented. Thus Decaisne placed Plantago princeps next to P. fernandeziana of Juan Fernandez; whilst according to Hillebrand, Plantago pachyphylla resembles P. aucklandica from the Auckland Islands. These resemblances are consistently associated with the respective range in altitude of the Hawaiian plants, since Plantago princeps occurs usually between 2,000 and 4,000 feet, and P. pachyphylla between 6,000 and 8,000 feet, the species of greatest elevation being related with the species of highest latitude. It is thus seen that these endemic mountain genera with peculiar species have

very evident affinities with the plants of extra-tropical southern latitudes, and especially with the "Antarctic" flora. This affinity will also be found, as will subsequently be noticed, in the case of genera like Cyathodes and Nertera, where there is still a specific connection with the outside world.

THE MOUNTAIN-FLORA OF HAWAII, AS REPRESENTED BY THE NON-ENDEMIC GENERA (Compiled from Hillebrand's Flora).

Genus	Usual altitude of station in feet.	Distribution outside Polynesia.					Distribution in Hawaii, Fiji, and Tahiti.				Fruit.
		Both Worlds.	Old World.	New World.	Antarctic flora.	Australia and New Zealand.	Hawaii only.	Hawaii, Fiji.	Hawaii, Tahiti.	All three groups.	
						WITH ALL SPECIES ENDEMIC.					
Ranunculus (2) ...	6,000— 7,000	+	......	......	......	......	+	......	......	......	Achene.
Viola (5)	2,000— 6,000	+	......	......	......	......	+	......	......	......	Capsule.
Silene (4)	2,000— 9,000	+	......	......	......	......	+	......	......	......	Capsule.
Geranium (6)	5,000—10,000	+	......	......	......	......	+	......	......	......	Carpels.
Vicia (1)	7,000— 8,000	+	......	......	......	......	+	......	......	......	Pod.
Sophora (1)	5,000—10,000	+	......	......	......	......	......	......	......	+	Pod.
Rubus (3)............	4,000— 7,000	+	......	......	......	......	......	+	......	......	Berry.
Acæna (1)	5,000— 6,000	......	......	......	+	......	+	......	......	......	Spinose achene.
Gunnera (1)........	3,000— 6,000	......	......	......	+	......	+	......	......	......	Drupe.
Sanicula (1)........	6,000— 8,000	......	......	+	......	......	+	......	......	......	Prickly carpel.
Coprosma (9)	3,000— 9,000	......	......	......	......	+	......	......	......	+	Drupe.
Lagenophora (1)...	6,000	......	......	......	+	......	......	+	......	......	Viscid achene.
Artemisia (2)	4,000— 8,000	+	......	......	......	......	+	......	......	......	Achene.
Lobelia (5)	2,000— 6,000	+	......	......	......	......	+	......	......	......	Capsule.
Vaccinium (2)......	3,000— 8,000	+	......	......	......	......	......	......	......	+ Samoa	Berry.
Myoporum (1) ...	Coast to 10,000	......	......	......	......	+	+	......	......	......	Drupe.
Plantago (2)	2,000— 8,000	+	......	......	......	......	+	......	......	......	Capsule.
Exocarpus (2)......	3,000— 6,000	......	......	......	......	+	+	......	......	......	Fleshy nut.
Sisyrinchium (1)...	4,000— 7,000	......	......	+	......	......	+	......	......	......	Capsule.
Astelia (2)	2,000— 6,000	......	......	......	+	......	......	......	......	+	Berry.
Oreobolus (1)	6,000	......	......	......	+	......	+	......	......	......	Toothed nutlet.
Uncinia (1)	3,000— 5,000	......	......	......	+	......	+	......	......	......	Awned nutlet.
Agrostis (3)	4,000— 6,000	+	......	......	......	......	+	......	......	......	Awned grain.
Deschampsia (3)...	3,000— 6,000	+	......	......	......	......	+	......	......	......	Awned grain.
Trisetum (1)	3,000— 5,000	+	......	......	......	......	+	......	......	......	Awned grain.
Poa (2)		+	......	......	......	......	+	......	......	......	Grain.
						WITH ENDEMIC AND NON-ENDEMIC SPECIES.					
Cyathodes (2)......	2,000—10,000	......	......	......	......	+	......	......	+	......	Drupe.
Lysimachia (6) ...	Coast to 6,000	+	......	......	......	......	+	......	......	......	Capsule.
Chenopodium (2)..	Up to 7,000	+	......	......	......	......	+	......	......	......	Seed-like.
Santalum (3)	Coast to 10,000	......	+	......	......	......	......	......	......	+	Drupe.
Carex (5)	2,000—7,000	+	......	......	......	......	......	+	......	......	Nutlet.
Rhynchospora (4).	Up to 10,000	+	......	......	......	......	......	......	......	+	Nutlet.
Panicum (14)	Coast to 6,000	+	......	......	......	......	......	......	......	+	Grain.
Deyeuxia (3)	Up to 10,000	+	......	......	......	......	+	......	......	......	Awned grain.
						WITH NO ENDEMIC SPECIES.					
Fragaria chilensis.	4,000— 6,000	......	......	+	......	......	+	......	......	......	Fleshy.
Drosera longifolia.	4,000	+	......	......	......	......	+	......	......	......	Capsule.
Nertera depressa..	2,500— 5,000	......	......	......	+	......	......	......	......	+ Samoa	Drupe.
Luzula campestris.	3,000—10,000	+	......	......	......	......	......	......	+	......	Capsule.

It is evident that in one or two cases the connection between the representatives of the "Antarctic" genera on the Hawaiian uplands and those of high southern latitudes has only been recently broken off. Thus with reference to the Hawaiian species of the Cyperaceous genus, Uncinia, it may be observed that although Hillebrand regards it as a distinct species, Hemsley (*Intr. Bot. Chall. Exped.*, p. 31) remarks that it is very near if not the same as a New Zealand species, an affinity very significant of the source of the mountain plants of this group that are derived from these southern latitudes.

The next component to be recognised in these Hawaiian mountain genera with peculiar species is a small special American element; and in this connection Sanicula and Sisyrinchium may be especially mentioned. The first is mainly North American, and particularly Californian; but there are two solitary species found on the continents and in oceanic islands such as the Azores. The continental species, Sanicula europæa, occurs not only in Europe and Central Asia, but in South Africa, and at high elevations on the mountains of Equatorial Africa and of Madagascar. It is not, however, with this widely ranging species that Sanicula sandwicensis is related, but with S. menziesii, a species from California and Oregon (Hillebrand). Sisyrinchium is confined to temperate and tropical America; but a singular and suggestive outlier of the genus (S. bermudiana) is found in Bermuda.

The mountain genera that are distributed on both sides of the Pacific constitute about three-fifths of the total. So far as my scanty data show, they seem to have reached Hawaii from the four quarters of the compass. The probable southerly origin of Plantago has been already indicated. Hillebrand notes the great resemblance between Lobelia gaudichaudii and an undescribed species from the Liukiu Islands, lying on the west side of the Pacific. It is likely, also, that the genus Ranunculus reached Hawaii from the west, since one of the species, R. mauiensis, resembles R. repens of the Old World (Hillebrand); whilst the other, R. hawaiiensis, comes near R. sericeus of Mauritius (Drake del Castillo). On the other hand, the genus Rubus may hail from an American source, since, in the opinion of Gray, Rubus hawaiiensis, one of the mountain raspberries, finds its nearest relative in R. spectabilis from the north-west coast of America; and there are reasons for believing, as will subsequently be shown, that the genus Artemisia has an American source. It is also probable that some of these genera have reached Hawaii from the

north, since it is likely, as pointed out in a later page, that the Carices of the Hawaiian uplands came originally from north-eastern Asia.

In the previous paragraphs the mountain genera have been considered with especial reference to their distribution and source beyond the confines of the Pacific. If we now briefly discuss them from the standpoint of their distribution within the Pacific, or rather as concerning their presence or absence in the Fijian and Tahitian groups, we shall see that to a large extent Hawaii has received its mountain genera of this era independently of the other Pacific groups.

Mountain genera possessing only peculiar species,	in Hawaii only . . .	20
" " " "	in Hawaii and Fiji . .	2
" " " "	in Hawaii and Tahiti .	0
" " " "	in all three groups . .	4
		26

It is here shown that three-fourths of the genera of the Hawaiian mountains in this era are not found either in Fiji or Tahiti. This, as before pointed out, is mainly to be attributed to the greater elevation of the Hawaiian Islands. Had there been an island 13,000 to 14,000 feet in height in Fiji, we cannot think that any such contrast in the floras would have existed. The temperate genera of the Hawaiian uplands would have been largely represented in the Fijian flora. Yet although we do not find such genera as Ranunculus, Geranium, Sanicula, Uncinia, &c., in Fiji and Tahiti, a small number of the Hawaiian mountain genera have obtained a scanty footing. This is what we might have expected. Thus, Lagenophora has been found on the mountains of Vanua Levu, and Vaccinium in Tahiti and Rarotonga; whilst Coprosma and Astelia occur on the tops of some of the mountains in both regions. In Fiji their distribution seems sporadic, as shown not in Lagenophora alone, but also by Astelia, which has been found only on the summit of Kandavu.

The Capacities for Dispersal of the Hawaiian Non-endemic Mountain Genera possessing only Peculiar Species.—As shown in the Table, seven, or 27 per cent., of these genera have fleshy fruits that would attract frugivorous birds. In three cases (Gunnera, Coprosma, Myoporum) they are drupes, in three others (Rubus, Vaccinium, Astelia) they are berries, and in one (Exocarpus) there is a nut with a fleshy perigone. It is particularly interesting to notice that frugivorous birds, and I include here granivorous

birds that are known to be frugivorous at times, could have transported seeds of the "Antarctic" flora to this group. We can observe the process in operation in our own time within the limits of the group. It has been long known, and we find it referred to in the pages of Hillebrand's work, that the wild mountain-goose (Bernicla sandwicensis) feeds upon the fruits of Coprosma ernodeoides, and of Vaccinium reticulatum, the famous "ohelo." The fruits of the first are known to the natives as "kukai neenee" (droppings of geese), and the hard stones or pyrenes are very well suited for withstanding the risks of the digestive process. I found a number of these pyrenes in the stomach of a mountain-goose shot by my companion, Dr. Krämer, high up the slopes of Mauna Loa.

According to Mr. Perkins, Chloridops kona, a big Hawaiian finch, feeds on the fruits of the bastard sandal-tree (Myoporum sandwicense). There are no "impossible fruits" among the mountain genera of Hawaii, that is to say, fruits so large that bird agency must be excluded. All of them are practicable in point of size. Thus amongst the largest, the "stones" of Gunnera would not exceed $\frac{1}{5}$ of an inch (5 mm.), and those of Myoporum scarcely $\frac{1}{4}$ of an inch (6 mm.); whilst the nuts of Exocarpus range in the Hawaiian species from $\frac{3}{10}$ to $\frac{6}{10}$ of an inch (7–15 mm.), and the beans of Sophora chrysophylla do not at the most exceed $\frac{1}{4}$ of an inch (6 mm.).

The principal feature, however, which these mountain genera exhibit from the point of view of their dispersal is the number of plants possessing seeds or fruits capable of adhering to plumage. Half of these genera are thus characterised. Of these Sanicula and Acæna represent the ordinary hooked fruits; whilst the fruits of the Grasses and Sedges, Agrostis, Deschampsia, Trisetum, Poa, Oreobolus, and Uncinia, are enabled by means of their awns or of their serrated beaks to attach themselves to plumage, and the same may be said of the carpels of Geranium. The fruits of Lagenophora and the seeds of Plantago display the capacity of adhesiveness by means of a gummy secretion.

One or two of these genera need further mention. I will first take Acæna, which is spread all over the south temperate zone both on the continents and on the islands. The Hawaiian species (A. exigua) forms tussocky growths on the swampy summits of Mount Eeka in Maui, and in Kauai, at an elevation of 6,000 feet above the sea. Numerous observers refer to the probable mode of dispersal of the genus in the "Antarctic" and neighbouring islands.

Captain Carmichael, in the instance of Acæna sanguisorbæ on Tristan da Cunha, observes that it overruns the low ground. Its burr-like fruit, as he describes, "fixes itself on the slightest touch into one's clothes, and falling into a hundred pieces covers one all over with an unseemly crust of prickly seeds not to be got rid of without infinite labour" (*Trans. Linn. Soc.*, xii. 483, 1818). Both Mr. Moseley (Wallace's *Island Life*, p. 250) and Dr. Kidder (*Bull. U.S. Nat. Mus.*, 2) refer to the burrowing habits of the Petrels, Puffins, and other sea-birds amongst the vegetation covering the ground in Tristan da Cunha, Marion Island, Kerguelen, &c., in places where Acæna, amongst other plants, thrives. Mr. Moseley remarks that the fruits of this genus stick like burrs to feathers, and he looks to sea-birds for the dispersal of this and similar plants over the ocean. He especially notes that the Petrels and other seafowl burrow and breed high up the mountain-slopes of tropical islands as in Tahiti, Viti Levu, Hawaii, and Jamaica. . . . It should be noted in the case of the Hawaiian endemic species that it has been found only on two mountain tops; and that however active may be the dispersal of the genus in south temperate latitudes now, the Hawaiian Islands lie outside the present area of dispersal.

The next mountain genus I will specially refer to is Lagenophora, one of the Compositæ. The solitary Hawaiian endemic species, L. mauiensis, is restricted to the summit of Mount Eeka, in Maui. In the mountains of Vanua Levu, Fiji, another peculiar species, L. pickeringii, has been found; and there is a species, L. petiolata, in the Kermadec Islands (Hooker, in *Journ. Linn. Soc.*, i. 127); but the genus is chiefly characteristic of Australia, New Zealand, and temperate South America, one species occurring both in Fuegia and Tristan da Cunha. The genus has no pappus; but Hooker in the case of the Kermadec species considered that the "viscid fruit" favoured its dispersal; and this may probably be true of the genus.

With regard to the capacity for dispersal of the seeds of Plantago, it may be pointed out that the seeds of Plantago major, P. lanceolata, &c., become coated with a mucilaginous material when wetted. In 1892, when experimenting on these plants, I found that the wetted seeds adhered firmly to a feather, so that it could be blown about without their becoming detached. Species of Plantago are so characteristic of the "alpine" floras of the summits of lofty mountains in the tropics, as in Java and many other regions, that the mode of dispersal has always been a subject

of curiosity. I cannot myself doubt that this is the explanation of the occurrence of the representatives of the genus that now thrive as endemic species on the higher slopes of the Hawaiian mountains. This method of dispersal for Plantago is recognised by recent writers on the subject of seed-dispersal. (In a paper in *Science Gossip* for September, 1894, I dealt with the "mucous adhesiveness" of such seeds as a factor in dispersal. The subject had previously been discussed by Kerner in one of the earlier volumes of his *Pflanzenleben*; and I have summed up some of the results in Note 43 of the present volume.) My readers can readily ascertain by a simple experiment that a bird pecking the fruit-spikes in wet weather would often carry away some of the sticky seeds in its plumage. Several years ago, when I was endeavouring to examine the condition of these seeds in the droppings of a canary, my efforts were defeated by the bird itself, since, in spite of all my care, some seeds and capsules were always carried by the bird on its feathers into the clean cage reserved for the experiment.

The plants of these mountain genera possessing dry seeds or fruits neither very large nor very minute and suitable for bird-food are Ranunculus, Viola, Vicia, Sophora, Artemisia, Sisyrinchium, six in all, or 24 per cent. of the total. On the probable method of transport of the ancestors of these endemic species the following remarks may be made. With regard to Ranunculus, some authors like C. M. Weed (*Seed-Travellers*, p. 48, Boston, 1899) perceive in the curved or hooked beaks of the achenes a means of attaching the fruit to plumage. This no doubt applies to some species, and it is advocated by Ekstam for some of the plants of the Nova Zembla flora. There are others to which this explanation would not be applicable, and the achenes of the Hawaiian species do not appear to be specially fitted for this mode of transport. I have found the achenes of Ranunculus frequently in the stomachs of birds in England, in partridges frequently, and in wild ducks at times. Those of certain species that possess buoyancy are common in the floating seed-drift of rivers, as of the Thames (*Journ. Linn. Soc. Bot.*, xxix. 333), and they would probably in this way be often swallowed by waterfowl.

I have but few data directly relating to the dispersal of seeds of Viola by birds. From the frequent occurrence of species in alpine floras, as in the Caucasus, the Great Atlas, in the mountains of Equatorial Africa, in Madagascar, &c., it may be inferred that birds transport the seeds between the higher levels of many continental ranges in tropical regions and to the mountain-slopes

of neighbouring large islands. Viola abyssinica, for instance, which occurs in Madagascar, is spread over the elevated mountain ranges of tropical Africa. With regard to the five Hawaiian species, it may be remarked that three of them are bog species and two occur in dry situations. The first are most characteristic of the mountains, one species occurring on the summit of Mount Eeka, 6,000 feet above the sea. Judging from the stations alone, at least two species were originally introduced into the Hawaiian Group.

Viola seeds, as indicated by my experiments on the different British species, including Viola palustris, are not buoyant, and there is no possibility of the seeds being picked up by birds in floating drift. There is, however, a possible means of dispersal in birds' plumage by means of the mucosity of the seeds of some species. Thus, although this is not exhibited, as shown by my experiments, by Viola canina and V. palustris, it is well displayed by the Field-Pansy (V. tricolor). I found that the seeds of this species, after lying a little time in water, were thickly covered with mucus, and that they adhered to a feather, on drying, as firmly as if gummed. This did not, however, come under my notice in the case of the seeds of one of the Hawaiian species, V. chamissoniana, examined by me. One sometimes observes Viola canina in England growing in places, as in the crevices and on the tops of old walls, where its seeds could have only been carried by birds. In some cases the propellent force of the seed ejected by the contracting valves of the capsule would explain queer stations. In its power of seed-expulsion, Viola chamissoniana, the common Hawaiian species, is just as active as our British species.

With regard to the Leguminous genus Vicia we have the observation of Focke on the dispersal of its seeds by pigeons, as described before on page 150.

Sophora chrysophylla, the "Mamani" of the natives and one of the most familiar of the trees of the Hawaiian mountains, is discussed at length in Chapter XV., where the difficulty of supposing that its seeds could be transported unharmed in a bird's stomach half-way across the Pacific is pointed out; and it is suggested that it was more probably derived from a littoral species brought by the currents. However, the point is a debatable one, and the seeds of the "Mamani" can scarcely be regarded as "impossible" from the standpoint of dispersal.

With reference to the possibilities of dispersal of the achenes of Artemisia, some very suggestive indications are to be obtained from a paper by Mr. D. Douglas on the North American Tetra-

onidæ published in the *Transactions of the Linnæan Society* for 1833. The "Cock of the Plains" (Tetrao urophasianus), as we here learn, makes its nest on the ground under the shade of Artemisia bushes, and lives on the foliage and fruits of these and other plants. This bird is plentiful in Columbia and North California, and another allied species is mentioned which lives on the same sort of food. Later authors refer to these and other birds of the same family as living chiefly on the Sage-brush (Artemisia tridentata), a plant prevailing over great regions of the plains as well as on the slopes of the Sierra Nevada and of the Rocky Mountains. According to Dr. Sernander (page 228), birds when feeding on the fruits of Artemisia vulgaris in the district of Upsala scatter them about and thus aid in its dispersal. Artemisia achenes, since they have neither pappus nor other appendages, nor any special adhesiveness when wetted, depend largely on their small size and light weight to aid them in dispersal. (Those of A. absinthium measure a millimetre in length, or $\frac{1}{25}$ of an inch, whilst those of A. vulgaris measure 1·8 mm., or $\frac{1}{14}$ of an inch.) Driven as we are to look to bird-dispersal for the means of transport of Artemisia achenes, it is interesting to find a possible source of the Hawaiian endemic species on the nearest American mainland, even though it is some 2,000 miles away. It is assumed that they would be ordinarily carried in adherent soil or entangled in the feathers, and on rare occasions in the bird's stomach.

The small seeds of Sisyrinchium possess no means of adherence to plumage. They are crustaceous, and in cases where the stomach and intestines of a bird are well filled with other food they are quite capable of resisting injury. The solitary Hawaiian species has, according to Hillebrand, a range in altitude from 3,500 to 7,000 feet. I found this pretty herb most abundant on the "cattle-plains" of Hawaii between 5,000 and 6,000 feet, where it is evidently in part dispersed by the cattle and other animals. The seeds are very small, being about a millimetre in size, and when dried nearly 100 go to a grain (0·65 decigramme). They might thus also be transported in mud on birds' feet.

For the mode of dispersal of the minute seeds of Lobelia, the last of the mountain genera to be specially noticed, I must refer the reader to the remarks on this subject in Chapter XXII. They would probably be carried in soil adhering to the legs or feet of a bird.

There are one or two interesting points relating to the temperate genus Silene, which is represented on these mountains. The four

Hawaiian species show a great range in altitude. Thus, whilst S. struthioloides finds its home in Hawaii and Maui at elevations of 5,000 to 9,000 feet, another species (S. lanceolata) thrives equally at elevations of 5,000 or 6,000 feet on the central plateau of Hawaii and at heights only of 300 to 500 feet above the sea. Although I have not yet come upon any direct reference to the mode of dispersal of the small seeds of this genus, there is little doubt that their rough tuberculated surfaces would favour their attachment to plumage. A very significant observation, however, is made by Jens Holmboe in a paper on littoral plants in the interior of Norway. He refers to the occurrence in no small quantity of Silene maritima on the top of "Linnekleppen," 331 metres high, one of the highest peaks of Smaalenene, and distant about 29 kilometres from the nearest coast (*Strandplanter i det indre af Norge*, "Naturen," Bergen, 1899). Sernander (p. 405), commenting on this observation, remarks that since bare hill-tops are frequented by birds, such an agency in this instance is not impossible.

I will conclude these remarks on the non-endemic Hawaiian mountain genera possessing only peculiar species, with a few observations on the genus Vaccinium in the Pacific. This genus is known to be distributed over the northern hemisphere and to occur on the uplands of tropical mountains, as, for instance, on the summits of the Java mountains and on the high levels of the Equatorial Andes at altitudes even of 15,000 to 16,000 feet. There are apparently only some four or five species known from the Pacific islands, from Hawaii, the Marquesas, Tahiti, Rarotonga, Samoa, and the New Hebrides, and it would almost seem that these can be reduced to one or two species. Although not yet recorded from Fiji, the probability of the genus being represented on some of the mountains is pointed out by Seemann. Of these Pacific forms a single species, V. cereum, is spread over the East Polynesian region including the Marquesas, Tahiti, and Rarotonga; and, according to Hillebrand, V. reticulatum, one of the two endemic Hawaiian species, is nearly related to it. Even the New Hebrides species (V. macgillivrayi) resembles it, according to Seemann, in general appearance. That there has been a single Pacific polymorphous species is, as shown below, not impossible; but Reinecke, in describing in 1898 the Samoan species, V. antipodum, was under the impression that it was the only species known from the southern hemisphere, and says nothing of its affinity to other Pacific plants.

A few words on the station and habit of Vaccinium in the Pacific islands may be here of interest. In Hawaii there are, according to Hillebrand, two species, a high-level form, V. reticulatum, occurring at elevations of 4,000 to 8,000 feet, and a low-level form, V. penduliflorum, ranging between 1,000 and 4,000 feet. I may, however, remark that the last species occasionally came under my notice at elevations of 6,000 to 7,000 feet. This species exhibits much variation, and Gray, Wawra, and other botanists have evidently not been always able to distinguish between the two species in their varying forms. It is not only distinguished from the high-level species by its lower station, but also by its epiphytic habit, a circumstance that, as pointed out below, may explain some of the differences, since such a habit is bound up with the difference in station. It seems, therefore, safer to regard them as station forms of one species which is closely allied to V. cereum, the species of the South Pacific, an inference which, if well founded, would make highly probable the view that there has been a single polymorphous Pacific species. . . . In Tahiti, as we learn from Nadeaud, V. cereum occurs on the mountain-tops at altitudes exceeding 800 metres (2,600 feet). In Rarotonga, according to Cheeseman, it is found on the summits of most of the higher hills extending almost to the summit of the island, 2,250 feet above the sea. The Samoan species, V. antipodum of Reinecke, which that botanist considers as probably one with V. whitmei, a Polynesian (Samoa?) species originally described by Baron F. von Müller, grows in the central mountains of Savaii at an elevation of 1,500 metres (4,920 feet).

These Pacific species of Vaccinium, as on tropical mountains of the continents, occasionally assume an epiphytic habit, and it is here, as above observed, that lies one of the distinctions between the Hawaiian species. V. penduliflorum, the low-level form, occurs typically in the forests, where, according to Hillebrand, it grows on the trunks of old trees. The trees, however, may be quite in their prime, and I have observed it growing in the fork of the trunk of an Olapa tree (Cheirodendron gaudichaudii). It is in this connection of significance to notice that a variety found in open glades and on grassy slopes is described by Hillebrand as terrestrial in habit. The other high-level form, V. reticulatum, grows gregariously on open ground, and is typically terrestrial in its habit. The Samoan species, as we learn from Reinecke, grows on trees, as on the branches of Gardenia. The epiphytic habit of species of Vaccinium is especially discussed by Schimper in the case of plants

growing on the Java mountains. He there shows (*Plant-Geography*, i. 14) that species which are epiphytes in the virgin forest become terrestrial plants in the treeless alpine region. This interchange of station, which is exhibited by several other plants, including orchids and ferns, is connected with their xerophilous characteristics, and is given by Schimper as an example of the interchange of physiologically dry habitats.

Of the mode of dispersal of Vaccinium by frugivorous birds, much has been written and much will be familiar to my readers. The berries of V. reticulatum are known to be the principal food of the Hawaiian mountain-goose. But probably birds of the grouse family have been the chief agents in distributing the genus over the continents. I have frequently found the fruits in the stomachs of the Black Cock (Tetrao tetrix), the Scotch Grouse (Lagopus scoticus), and the Capercailzie (Tetrao urogallus); but the same story comes from all over the northern hemisphere. The Willow Grouse (Lagopus albus), which travels round the globe, is known to feed on them. Hesselman in Sweden and Ekstam in Nova Zembla have especially investigated the dispersal of Vaccinium by Tetrao tetrix and Lagopus (see Sernander, pp. 6, 226); and according to Mr. Douglas and others the different species of Tetrao that frequent the subalpine regions of the Rocky Mountains and the uplands of Columbia and North California subsist on Vaccinium fruits. This family is not now represented in the Hawaiian avifauna; but it is noteworthy, as indicated by the differentiation of the Pacific species of Vaccinium, that dispersal of the genus is there almost suspended except within the region of Eastern Polynesia. It is probable that numerous other birds, except the Hawaiian goose, aided the original dispersal.

The Mountain Genera with both Endemic and Non-endemic Species.—I pass on now to consider those Hawaiian mountain genera that possess species some of which are confined to the group, whilst others occur in regions outside the islands. They are not many, as may be seen from the table before given, and but few of them are entirely restricted to the high levels, a range in altitude that may be frequently associated with great lateral extension of the genus over different latitudes. Here the agents of dispersal have through some species in each genus preserved a connection with the outer world, though it may be restricted to the limits of the Pacific islands.

Cyathodes tameiameiæ, an Epacridaceous species found also in the uplands of Tahiti, occurs, according to Hillebrand, on all the

Hawaiian Islands, from 1,800 feet up to the limit of vegetation 10,000 feet and over above the sea. I found it, however, at even lower levels. On the Puna coast of Hawaii, associated with Metrosideros polymorpha, Osteomeles anthyllidifolia, and other inland plants, it descends on the surface of ancient lava-flows to the coast wherever the bolder spurs reach the sea-border. The other species, C. imbricata, is more exclusively confined to the greater altitudes. It is endemic, and may possibly be a station form of the other species.

The six species of Lysimachia are found at different elevations, one near the sea-shore, others at altitudes of 2,000 to 3,000 feet, and others again at elevations of 6,000 feet. Chenopodium sandwicheum occurs at all elevations from near the coast to the high inland plains of Hawaii and to the upper slopes of Mauna Kea, that is to say, up to altitudes of 6,000 or 7,000 feet. Hillebrand observes that it is a low decumbent plant at the coast, and may become arborescent with a height of 12 to 15 feet in the upper forests of Mauna Kea.

The species of Santalum (sandal-wood trees) also display great vertical range in these islands. Though S. freycinetianum, which is also a Tahitian species, is most at home in the forests 2,000 to 4,000 feet above the sea, it has, as Hillebrand informs us, a dwarfed form that extends far up the mountain slopes of Mauna Loa and Hualalai to elevations of 7,000 or 8,000 feet, and another dwarfed shrubby variety that grows only near the sea-shore. Another species, S. haleakalæ, occurs as a tall shrub on Haleakala at elevations of 8,000 to 10,000 feet. Among the sedges, most of those of the genera Carex and Rhynchospora are found at altitudes of between 3,000 and 7,000 feet, and two grasses of the genus Deyeuxia occur at elevations of 6,000 to 8,000 feet.

Amongst these Hawaiian mountain genera with both endemic and non-endemic species there are no plants possessing fruits which from their size could be with difficulty regarded as dispersed by birds. The mode of dispersal of these plants is in some cases indeed not far to seek. Thus in the stomach of an Hawaiian goose (Bernicla sandwicensis), shot by my companion Dr. Krämer on the slopes of Mauna Loa, I found a number of the "stones" of Cyathodes tameiameiæ, the plant being abundant in fruit in the immediate vicinity. It is highly probable that the seeds of Santalum have been carried over the Pacific by frugivorous birds. We learn from Dr. Brandis that Santalum album in India is mainly spread through the agency of birds (*Bot. Chall. Exped.*, iii. 13).

The drupes of the Pacific species, S. freycinetianum, that occurs alike in Hawaii, the Marquesas, and Tahiti (Drake del Castillo), measure about half an inch. There can be little doubt that with this tree, as with the species of Cyathodes above mentioned, which also links together Tahiti and Hawaii, there has been up to recent times an interchange by means of frugivorous birds between these two regions, some 2,000 miles apart.

The small seeds of the capsular fruits of Lysimachia could be transported in birds' plumage or in dried soil attached to their feet or feathers. The seed-like fruits of Chenopodium were probably dispersed by some granivorous bird, much as nowadays our partridges carry about in their stomachs the similar fruits of Atriplex. The long-awned fruits of Deyeuxia were, it is likely, transported in birds' plumage, and doubtless also those of Panicum ; whilst the nutlets of Carex and Rhynchospora might have been carried about in a similar fashion.

The distribution of the non-endemic species of these Hawaiian mountain genera may perhaps aid us in determining the original source of the genus as well as in confirming the conclusions formed concerning the other mountain genera that only possess species restricted to the group. Lysimachia, Chenopodium, Carex, Rhynchospora, Deyeuxia, and Panicum are found in both the Old and New Worlds. Since Hillebrand remarks that one of the six species of Lysimachia (L. spathulata) occurs in Japan and in the Liukiu, Bonin, and Marianne groups, we have here a valuable indication of the route followed by a genus that has not been recorded from the oceanic groups of the South Pacific.

The capricious distribution of the genus Carex in the Pacific is remarkable, and it is noticed by Hemsley in the Introduction to the *Botany of the "Challenger" Expedition*. No species have been recorded from Tahiti, the Marquesas, and Rarotonga, but three Fijian species are mentioned by Hemsley, and there is another in Samoa. Of the five Hawaiian species given by Hillebrand, two are endemic. Of the rest, C. wahuensis (oahuensis), Meyer, occurs also in Korea and Japan, whilst C. brunnea, Thunb., is found in Japan and Australia, and the third, C. propinqua, Nees., occurs all round the border of the Pacific Ocean, from Kamschatka through Alaska south to the Straits of Magellan. These three species all possess a home in common in north-east Asia, and probably there lies the source of the Hawaiian species of Carex—a conclusion which would help to explain the irregular distribution of the genus amongst the South Pacific groups.

The genus Rhynchospora occurs alike in the Hawaiian, Tahitian, and Fijian islands; but the groups in the North and South Pacific seem to have been independently supplied with the original species, since R. aurea, a widely spread tropical species, ranging the South Pacific from New Caledonia to Tahiti, has not been recorded from Hawaii. A connection between Hawaii and the Australian region seems to be indicated by a species of Deyeuxia (D. forsteri) that is found also in Easter Island, Australia, and New Zealand, and by the presence of the Australian and New Zealand genus Cyathodes in Hawaii, though the existence of a species common to both Tahiti and Hawaii goes to show that the route followed by the genus lay through Eastern Polynesia. It is also not unlikely that the genus Santalum reached Hawaii through Eastern Polynesia, since two forms found in Hawaii and Tahiti are closely allied, and are, in fact, regarded by Drake del Castillo as the same species. The genus occurs in tropical Asia, Australia, and New Zealand.

Looking at the indications above given, I should be inclined to think that the genera Lysimachia and Carex reached the Hawaiian mountains from temperate Asia or the islands off its Pacific coast, and that Cyathodes, Santalum, and Deyeuxia hail from the Australian or New Zealand region by way of Eastern Polynesia.

The Mountain Genera possessing no Endemic Species.—The few remaining mountain plants of Hawaii to be considered are solitary, widely ranging species of genera that here possess no peculiar species. Such may be regarded as belonging to the latest age of the indigenous plants. They still keep up, or kept up until recently, the connection with the world outside Hawaii, and among them one may name here Fragaria chilensis, Drosera longifolia, Nertera depressa, and Luzula campestris.

Fragaria chilensis, the Chilian strawberry, flourishes at elevations of between 4,000 and 6,000 feet on the Hawaiian mountains. Its fruits, according to Hillebrand and other authors, are much appreciated by the wild goose of the islands. This plant ranges in America from Chile north to Alaska; and Drake del Castillo is doubtless on safe ground when he assumes that a congener of this bird originally brought the species from the nearest part of the American continent, namely from California (*Remarques*, &c., p. 8). In this connection it should be remembered that one of the endemic mountain-raspberries of Hawaii (Rubus hawaiiensis) finds its nearest relative, according to Gray, in Rubus spectabilis, a species from the north-west coast of America.

The species of Sun-dew, Drosera longifolia, hitherto found only on the marshy tableland of Kauai at an elevation of 4,000 feet above the sea, occurs both in Asia and North America. Its minute fusiform seeds are very light in weight, and might readily become entangled in a bird's plumage, or they could be carried in adherent dried mud.

Luzula campestris, which grows on the high mountains of the Hawaiian group from 3,000 feet upward, is also found in Tahiti. It is widely distributed in cool latitudes, and there is no special indication of its source. Its seeds are especially well suited for adhering to birds' feathers. When experimenting on these seeds in 1893 I ascertained that whether freshly gathered or kept for more than a year they became on wetting coated with mucus, and adhered firmly to a feather on drying. There are many ways in which the "sticky" seeds in wet weather might fasten themselves to a bird's plumage. The plant-materials might be used, for instance, for making nests. The Sea Eagle (Aquila albicilla), as we learn from Mr. Napier (*Lakes and Rivers*), uses materials derived from Luzula sylvatica in the construction of its nest.

Nertera depressa, a creeping Rubiaceous plant, with red, fleshy drupes containing two coriaceous pyrenes, is found in all the Hawaiian Islands at elevations of 2,500 to 5,000 feet, and it grows on the mountains of Tahiti at altitudes over 3,000 feet. The genus is widely diffused over the southern hemisphere. This particular species is characteristic of the Antarctic flora, being found all round the south temperate zone (excepting South Africa) in New Zealand, Fuegia, the Falkland Islands, and Tristan da Cunha, and extending up the Andes to Mexico, occurring also on the summits of Malayan mountains at elevations of 9,000 to 10,500 feet above the sea, as on Pangerango in West Java (Schimper), and on Kinabalu in North Borneo (Stapf). Captain Carmichael, who resided on Tristan da Cunha in the early part of last century, states (*Trans. Linn. Soc.*, xii. 483) that its drupes are eaten by a species of thrush and by a bunting. Professor Moseley, who visited the island in the *Challenger* many years after, remarks that its fruits are "the favourite food of the remarkable endemic thrush, Nesocichla eremita," the bunting being Emberiza brasiliensis (*Bot. Chall. Exped.*, ii. 141). It would seem most likely that the Hawaiian Islands received this representative of the Antarctic flora through the Tahitian Islands, as in the case of the species of Cyathodes common to both these groups.

Looking at the indications of these four widely ranging plants,

the Chilian strawberry (Fragaria chilensis), the Sun-dew (Drosera longifolia), Nertera depressa, and Luzula campestris, it may be inferred that with the exception of Nertera they all reached Hawaii from either the Asiatic or American sides of the North Pacific, the last route being evident in the case of the strawberry. Nertera depressa was probably derived from southern latitudes.

Summary.

(1) The second era of the flowering plants of the Pacific islands is indicated by the non-endemic genera. Here also the isolating influences have been generally active, and the work of dispersal is in some regions largely suspended. Thus in Hawaii nearly half the non-endemic genera possess only species that are restricted to the group, whilst in Fiji and Tahiti about a fourth are thus isolated.

(2) The contrast in the elevations of the islands of the Hawaiian, Tahitian, and Fijian regions is reflected in the development of an extensive mountain-flora in Hawaii, in its scanty development in Tahiti, and, excluding the Fijian conifers, in a mere remnant in Fiji and Samoa.

(3) The influence of isolation has been very active in the Hawaiian mountains, since about two-thirds of the genera contain only species confined to the group, and are thus disconnected from the world outside.

(4) Amongst these disconnected Hawaiian mountain genera, Antarctic or New Zealand genera, like Acæna, Gunnera, Coprosma, and Lagenophora, constitute nearly a third. The American element, represented, for instance, by Sanicula and Sisyrinchium, is small; whilst the genera found on both sides of the Pacific form more than one-half of the total, and include genera like Ranunculus, Viola, Rubus, Artemisia, Vaccinium, and Plantago, that often represent the flora of the temperate zone on the summits of tropical mountains. Three-fourths of these genera are not found either in Fiji or in Tahiti.

(5) The proportion of the disconnected Hawaiian mountain genera possessing seeds or seedvessels suited for dispersal in a bird's plumage is very large, quite half belonging to this category; whilst only about a fourth have fruits that would be dispersed by frugivorous birds.

(6) The Hawaiian mountain genera that still remain in touch with the external world through species found outside the islands

whilst other species are confined to the group, present a later stage in the plant-stocking. Their widely ranging species, which would be dispersed either by frugivorous birds, as with Santalum and Cyathodes, or in birds' plumage, as with Lysimachia, Carex, and Deyeuxia, seem to indicate that the main lines of migration for these genera have been from temperate Asia and from the Australian and New Zealand region, the last by way of Eastern Polynesia.

(7) The latest stage of the Hawaiian mountain-flora is exemplified by those genera that are only represented in the group by a solitary widely-ranging species, such as Fragaria chilensis, Nertera depressa, Drosera longifolia, and Luzula campestris. It is our own age; and birds are shown to be actual agents in the dispersal of the two first-named species and to be probable agents with the two other species. The two last-named species probably reached Hawaii from one or other side of the North Pacific; whilst Fragaria chilensis doubtless hails from the adjacent part of the American continent, and Nertera depressa from high southern latitudes by way of Tahiti.

CHAPTER XXIV

THE MOUNTAIN-FLORAS OF THE TAHITIAN AND FIJIAN REGIONS

The mountain-flora of the Tahitian region, as illustrated by the non-endemic genera.—Derived chiefly from high southern latitudes.—Weinmannia, Coprosma, Vaccinium, Astelia, Coriaria, Cyathodes, Nertera depressa, Luzula campestris.—The mountain flora of Rarotonga.—The mountain-flora of the Fijian region, as illustrated by the non-endemic genera.—Weinmannia, Lagenophora, Coprosma, Astelia, Vaccinium, Nertera depressa.—The Fijian Coniferæ.—Dammara, Podocarpus, Dacrydium.—Not belonging to the present era of dispersal.—The age of dispersal of the Coniferæ in the Pacific.—Earlier than the age of Compositæ and Lobeliaceæ.—The first in the Mesozoic period.—The last in the Tertiary period.—Summary.

THE MOUNTAIN-FLORA OF THE TAHITIAN REGION AS ILLUSTRATED BY THE NON-ENDEMIC GENERA

THIS floral region of the Pacific corresponds with the limits of Eastern Polynesia, and includes not only the Tahitian group proper, but also the Cook, Austral, Paumotuan, and Marquesan groups. It is only, however, in Tahiti, the peaks of which rise to over 7,000 feet above the sea, that we should expect to find such a mountain-flora, since the islands of the other groups are much lower, the highest of them in the Marquesan group barely exceeding 4,000 feet. Yet even in Tahiti it is not possible to speak of a mountain-flora in the sense that we attach to it in Hawaii. The elevated area of its interior is, as described in Chapter XIX., relatively very small; whilst, as Drake del Castillo points out, the conditions presented by the steep mountain-slopes rarely afford a hold for trees of any size, ferns often predominating in the higher levels. Still, we can observe the traces of such a flora, and it is in

this sense only that the term "mountain-genera" is used in relation with this group.

Mountain-Genera of the Tahitian or East Polynesian Region.

Weinmannia, Saxifragaceæ, from New Zealand. Coprosma, Rubiaceæ, from New Zealand. Vaccinium, Vacciniaceæ, from the northern hemisphere. Astelia, Liliaceæ, from New Zealand.	all species endemic.
Coriaria, Coriariaceæ, from New Zealand. . . . . . Cyathodes, Epacridaceæ, from New Zealand	some species endemic.

Nertera depressa, Rubiaceæ, a species of the Antarctic flora.
Luzula campestris, Juncaceæ, from the northern hemisphere.

The Tahitian non-endemic mountain-genera, though scanty in number, are of considerable interest to the student of plant-dispersal. Among those possessing only species that are confined to Eastern Polynesia, genera that would be regarded as belonging to a past era of dispersal, Weinmannia, Coprosma, Vaccinium, and Astelia may be mentioned.

Weinmannia, a Saxifragaceous genus of trees and shrubs, not represented in Hawaii, but recorded from almost all the elevated oceanic groups of the tropical South Pacific, as well as from the New Hebrides and New Caledonia, has its home in South America, more particularly in the Andes, and also occurs in New Zealand, Tasmania, and the Mascarene Islands. One can scarcely doubt that, as in the case of Coprosma, the Pacific Islands derived their species originally from high southern latitudes, as from New Zealand, the absence of the genus from Hawaii negativing an American origin. Of the two Tahitian species, one is peculiar to Tahiti, whilst the other, W. parviflora, which is conspicuous on the mountain-crests at elevations of 3,000 feet and over, occurs also in the Marquesas. Another species grows in abundance in the interior of Rarotonga. Samoa possesses two species, one of which, W. affinis, occurs in Fiji, and the other, W. samoensis, which frequents the mountains at elevations of 1,500 to 3,300 feet, is seemingly endemic. Fiji possesses four or five species of Weinmannia occurring at all altitudes up to 2,000 feet, of which some are evidently peculiar. The capsular fruits of this genus contain hairy seeds that would probably become entangled in a bird's plumage. Dispersal by birds is distinctedly indicated

in the curious observation of Dr. Reinecke in the case of the Samoan peculiar species. The seeds, he says, appear to germinate by preference on the bark of other trees, young plants growing epiphytically being of frequent occurrence.

There is some evidence that the species of Weinmannia, about ten in all, found in the tropical islands of the open Pacific are derived from one or two polymorphous species. As we learn from Mr. Cheeseman, the Rarotongan species, W. rarotongensis, has considerable affinity to several closely allied Polynesian species, and its nearest allies are a Fijian and Samoan species, W. vitiensis and W. samoensis. Possibly, he remarks, fuller materials may lead to the union of several of these forms under one species.

The interesting New Zealand genus Coprosma, which we have noticed in Hawaii, occurs also in the Tahitian region and Fiji; and it will be further discussed under the last-named locality. The genus Vaccinium has been previously dealt with in Chapter XXIII.

The Liliaceous genus Astelia may be considered as representing, like Coprosma, the Antarctic or New Zealand flora in the higher levels (usually) of the islands of the tropical Pacific, where it grows both on trees and on the ground. The genus, according to Hemsley, is chiefly at home in New Zealand, but is also found in Fuegia and in South-east Australia. It is represented in Hawaii, Tahiti, Samoa, and Fiji. In Hawaii there are two peculiar species ranging between 2,000 to 6,000 feet in elevation. The solitary Tahitian species, A. nadeaudi, is found in the central mountains of Tahiti, reaching to the crests of Mount Aorai, which attains a height of 6,700 feet. Fiji and Samoa possess a species in common, A. montana, which is only recorded by Seemann, from the summit of Kandavu, 2,750 feet above the sea; whilst in Samoa it frequents, according to Reinecke, moist coast districts. The fruits of Astelia are berries with crustaceous seeds that would be dispersed by frugivorous birds.

Amongst the Tahitian mountain-genera that possess species ranging far beyond this region as well as species confined to the group may be mentioned Coriaria and Cyathodes. It is to their non-endemic species that we look for further clues as to the general lines of migration by which the mountain-genera that only possess peculiar species reached this group. The evidence afforded by Coriaria is of some importance. The genus has not been recorded from Hawaii, and, so far as the collections of Seemann and Horne show, not from Fiji. It is found in the Mediterranean

region, the Himalayas, Japan, New Zealand, and Antarctic America, including Chile; and there are two particular species, C. ruscifolia and C. thymifolia, that occur in both cases in New Zealand and the adjacent islands and in South America (Introd. *Chall. Bot.* p. 53). The first of these, which is very common in Chile, exists also in Tahiti on the crest of Aorai, 6,700 feet above the sea. Drake del Castillo also describes a peculiar Tahitian species, C. vescoi, of which the altitude is not given. Here one is in doubt whether Tahiti derived its wide-ranging species from New Zealand or from Chile; but in the New Zealand home of Coprosma, another Tahitian mountain-genus, we are afforded the clue. The fruits of Coriaria possess fleshy cocci that attract birds, though it would seem that the seeds of plants of this genus are poisonous for man. Among the numerous fruits that form the diet of the New Zealand fruit-pigeon (Carpophaga novæ zealandiæ) are included, as we learn from Sir W. Buller in his *Birds of New Zealand*, those of the "tupakihi" or "tutu" shrub, which Kirk identifies with C. ruscifolia, the species that also occurs on the summit of Tahiti.

The Australian and New Zealand genus Cyathodes (Epacridaceæ) has been already noticed in the case of Hawaii (page 282). The two Tahitian species occur on the elevated mountain-ridges forming the summits of Tahiti, one of them, C. tameiameiæ, occurring also in Hawaii, and the other, C. pomaræ, being restricted to the group. I have shown that the fruits are dispersed by frugivorous birds, and I can only include the genus as another example of the representation of the New Zealand flora in Tahiti . . . . There remain of these so-called Tahitian mountain-genera the Antarctic Nertera and the north-temperate Luzula, each represented by a solitary widely ranging species, N. depressa and L. campestris, which I have fully discussed under Hawaii (Chapter XXIII), in which group they also occur.

When we look at the evidence of origin supplied by the four Tahitian mountain-genera possessing species that are found outside the group, namely Coriaria, Cyathodes, Nertera, and Luzula, we find that the first three hail from high southern latitudes, and more especially from New Zealand; and when with this clue in our hands we take up the four genera Weinmannia, Coprosma, Vaccinium, and Astelia, possessing only species restricted to the Tahitian region, we find that all but the third-named genus hail also from the south. It would thus appear that the element of the Antarctic flora is much more evident in the

Tahitian mountain-genera than with those of Hawaii. In the Hawaiian mountain-flora, excluding, of course, the endemic genera, it includes about a fourth of the mountain-genera, which number about thirty-eight or forty in all ; whilst in the Tahitian mountain-flora it comprises six out of the eight genera. It may, indeed, be said that the resemblance between the mountain-genera of Hawaii and Tahiti is mainly restricted to genera that are found in high southern latitudes, namely, Nertera, Coprosma, Cyathodes, and Astelia, the only other genera linking the mountain-floras of both groups together being Vaccinium and Luzula, which probably hail from high northern latitudes. The agency of the frugivorous bird is plainly marked in the case of five out of the six genera that connect the cloud-capped peaks of Tahiti and Hawaii. In two of these genera, Cyathodes and Nertera, the same species occurs in both archipelagoes.

The Mountain-flora of Rarotonga.—A word may here be said on the representation of these mountain-genera in Rarotonga, a small island 2,250 feet in height and about eight miles in length, which is, however, the most important island of the Cook group. The recent important explorations of Mr. Cheeseman show that its flora is essentially Tahitian in character. As in Tahiti, the early age of the Compositæ and Lobeliaceæ is well represented in the high levels by peculiar species of Fitchia and Sclerotheca which are discussed in Chapters XXI and XXII. On account, however, of its relatively low altitude and its small size, we could not expect any extensive representation of the eight non-endemic mountain-genera of Tahiti. Yet three of these occur, a Tahitian species of Vaccinium (page 281) growing on its summits, whilst peculiar species of Weinmannia (page 290) and Coprosma (page 295) are found in its interior. The prevailing condition of many of the genera growing in the higher levels is one of isolation, since other genera, like Pittosporum and Elæocarpus, only possess peculiar species; but seeing that in several cases the species are closely allied to others found in the Western Pacific, as in Samoa, Fiji, and the Kermadec group, it is apparent that the period of isolation has not long commenced.

THE MOUNTAIN-FLORA OF THE FIJIAN REGION.

Weinmannia, Saxifragaceæ, Fiji and Samoa. Lagenophora, Compositæ, Fiji. Coprosma, Rubiaceæ, Fiji. Astelia, Liliaceæ, Fiji and Samoa.	Derived from New Zealand or from the Antarctic flora.

Vaccinium, Vacciniaceæ, Samoa, from the northern hemisphere.
Nertera depressa, Rubiaceæ, Samoa, from the Antarctic flora.
Dammara, Coniferæ, Fiji.
Podocarpus, Coniferæ, Fiji and Tonga.
Dacrydium, Coniferæ, Fiji.
} Not as a rule belonging to the present age of dispersal.

But little can be said of the mountain-flora of Fiji, since on account of the relatively low elevation of the islands there are but few special mountain-genera ; and as a rule we find only here and there a solitary species on some isolated peak that recalls the upland flora of the Hawaiian mountains. "None of the mountains of Fiji," remarks Horne (page 60), "are high enough for an alpine flora to exist. Many of the plants found on the tops of the mountains are also found near the level of the sea. On the other hand sea-level plants may also be found on the tops of the hills."

Fiji lacks the endemic genera of Compositæ and of Lobeliaceæ that often give a character to the mountain-floras of the Hawaiian and Tahitian regions, though, as remarked in Chapters XXI and XXII., their absence involves something more than a question of station. We find, however, four genera of the Antarctic or New Zealand flora, Weinmannia, Lagenophora, Coprosma, and Astelia. The first-named genus possesses four or five species ranging up to 2,000 feet, some of which are endemic, and it has been already discussed in this chapter. The United States Exploring Expedition found a single species of Lagenophora (L. pickeringii) on the mountains of the Mathuata coast of Vanua Levu, and no other species seems to have since been found. The subject is dealt with in Chapter XXIII in the case of Hawaii, but it may be here observed that there is an Hawaiian mountain species, and that the route followed by the ancestor of the Fijian species from the New Zealand home of the genus is indicated by a species in the intermediate Kermadec group. The genus Astelia has been discussed on page 291. It is represented in Hawaii and in most of the oceanic groups of elevated islands. The solitary species, A. montana, discovered by Seemann on the summit of Kandavu in Fiji, has since been found in Samoa, and probably Mr. Horne's collections contain another species.

The Rubiaceous genus Coprosma needs a few special remarks, since a particular genus of birds seems to have been concerned in dispersing it in the South Pacific. About fifty species are enumerated in the *Index Kewensis*, and if we include a few other species from the collections of Hillebrand, Horne, Cheeseman,

&c., the total would be about sixty. Of these, about half are restricted to New Zealand, which may be justly regarded as the home of the genus, the rest being confined to Australia and the islands of the Pacific, excepting a Chilian and three or four Malayan species. Hawaii with its nine species, Tahiti with two, Rarotonga with one, and Fiji with two or three species represent approximately the distribution of the genus in the oceanic archipelagoes of the tropical Pacific. (It most probably exists on the high peaks of Samoa, though it has not yet been recorded from the group.) In all, or in almost all cases, the species are restricted to their particular groups, so that we may regard the dispersal of the genus over the Pacific as suspended, though, as will be observed below, the period of suspension in the South Pacific has not been of sufficient duration to obliterate the affinities of species in distant groups and to prevent us from tracing out the route followed by the genus.

This genus of temperate latitudes, which in its New Zealand home ranges from near the sea-level to the region of the alpine floras, finds its usual station in the tropics on the summits of mountains. Thus, on Mount Kinabalu, in Borneo, it is found at altitudes of 10,500 to 13,000 feet (Stapf), and on the mountains of East Java at elevations exceeding 9,000 feet (Schimper). In Hawaii its species grow at elevations ranging from 3,000 to 9,000 feet, and in Tahiti at altitudes of 2,600 to 3,300 feet; whilst in Rarotonga it grows in the hilly parts of the island, its elevation in Fiji not being recorded.

When we come to consider the route by which the genus (Coprosma) entered the tropical Pacific, we must remember that unless we establish some special connection with its New Zealand home it will always be open for any one to suggest that the genus might have been derived, like Vaccinium, from other regions than the south, as from the summits of the Malayan mountains. However, a curious connection has been discovered by Mr. Cheeseman in his examination of the Kermadec and Rarotongan floras, and it would indeed appear that he has traced the Rarotongan peculiar species to its New Zealand home. Thus, he says that Coprosma lævigata, his new Rarotongan species, is very closely allied to the Kermadec endemic plant, C. acutifolia, Hook., which itself comes near C. lucida, Forst., a New Zealand species. The connection between Rarotonga and New Zealand by way of the Kermadec group is rendered yet more probable by the occurrence of two New Zealand species of Coprosma in the Kermadec flora (*Journ.*

Linn. Soc. i. 1857; *Trans. Linn. Soc. Bot.* vi. 1903; *Trans. N.Z. Instit.* xx. 1887).

When speaking of the genus in Hawaii (page 275), mention was made of the inter-island dispersal of the fruits of one of the species by the native mountain-goose, Bernicla sandwicensis. We learn from Sir W. Buller's *History of the Birds of New Zealand* that when the Coprosma is in fruit the Swamp-Hens (Porphyrio melanotus) come out to feed on it. These birds, he says, are capable of prolonged flight; and I chance to have beside me a cutting from the *Field* of July 9, 1904, in which "Hy. S." refers to a Black-backed Porphyrio that was captured in 1876 four hundred miles off the coast of New Zealand. This genus, which is widely dispersed in the tropics, the birds being commonly known as Sultanas, Blue Gallinules, Purple Water-Hens, &c., has probably been a very important factor in the dispersal of plants, especially in connection with insular floras. The birds live on a variety of food. The Messrs. Layard observed that Porphyrio vitiensis, which abounds in the swamps of New Caledonia, fed on maize, yams, &c. (*Ibis*, 1882); whilst in the stomach of a bird of the same genus shot in the Rewa swamps in Fiji I found a number of the stony fruits of Scleria, a genus of the Cyperaceæ. According to Mr. Wiglesworth, each region in the South Pacific has its own species of Porphyrio. There is one in the Tahitian Islands, and another common to Fiji, Tonga, and Samoa; whilst New Caledonia and the New Hebrides have their species ("Aves Polynesiæ"). However, it is evident that the power of dispersing seeds from group to group is not quite suspended, since, as we learn from Sir W. Buller, the New Zealand species, above named as partial to Coprosma drupes, is distributed over Tasmania and Australia, and reaches also Niue and New Caledonia; whilst the Messrs. Layard evidently regarded one species as common to Fiji and New Caledonia.

It is doubtless to birds of this description that we owe some of the specific connections of Coprosma between groups of the Western Pacific. That the dispersal of the species over distant regions was recently in active operation is shown by the close affinity, according to Dr. Stapf, of two species growing on the summit of Kinabalu, the Bornean mountain, with certain species from New Zealand and South-east Australia. Other Rubiaceous species, like Nertera depressa, possessing Coprosma-like fruits and fitted for the same mode of dispersal, link the heights of Kinabalu with the flora of high southern latitudes.

Being included in the Fijian area, the scanty mountain-flora of Samoa may be here referred to. As in Fiji, the endemic genera of Compositæ and Lobeliaceæ are not to be found, but we find in the central elevated district of Savaii, which rises to over 5,000 feet above the sea, a peculiar species of Vaccinium (4,900 feet), the Antarctic Nertera depressa (4,000 feet), and two species of Weinmannia, a genus hailing probably from high southern latitudes.

The Fijian Coniferæ.

It has been found most convenient to discuss here these interesting plants, which belong in a general sense to the mountain-flora of this archipelago. That which the Fijian flora loses in interest in the eyes of the student of plant-dispersal in not possessing the mysterious Composite and Lobeliaceous genera of Hawaii and Tahiti, it regains in the possession of its genera of Coniferæ. If he felt loth to apply his empirical principles to the above-named Hawaiian and Tahitian endemic genera, he feels more than uneasy when he comes to deal with the three Coniferous genera of Fiji, Dammara (Agathis), Podocarpus, and Dacrydium.

These three genera represent an order that has not found a home either in Tahiti or in East Polynesia generally, or in the more distant Hawaii; and they present at first sight in their existence in Fiji a powerful argument in favour of the previous continental condition of the islands of the Western Pacific. But in advocating this view we should remember that it involves the original continuity of the Fijian land-area, not only with the neighbouring islands of the New Hebrides and of New Caledonia where these genera alike occur, but also with New Zealand, Tasmania, and Australia, where they sometimes attain a great development.

In Fiji these trees often chiefly form the forests of the larger islands, extending in the moister regions from near the sea to the mountain-tops, and being often abundant on the great mountain-ridges of the interior. It may be at once remarked that, viewed merely from the standpoint of dispersal, there is no great difficulty in regarding it as probable that the seeds of Podocarpus and Dacrydium have been dispersed by frugivorous birds over tracts of ocean 500 or 600 miles across. Dammara, however, so far as my Fijian observations show, possesses none of the means of dispersal

across oceans that we are at present acquainted with. The two first-named genera occur in South America as well as in the Australo-Polynesian region, some of the species in these two regions, though the Pacific Ocean divides them, being closely related. Dammara is, on the other hand, confined to a much more limited area, extending from New Zealand to Borneo. It is from the distribution of this genus that the continental theory derives its chief support.

Yet it may be remarked that something more than questions relating to the capacity for dispersal are involved here. This is at once indicated by the circumstance that although Podocarpus is known to be dispersed by frugivorous birds, it is not found in Polynesia east of Tonga, and the same may be said of Dacrydium, which does not occur east of Fiji. In this connection it is necessary to notice the intrusion of Araucaria into the tropical Pacific from Eastern Australia to New Caledonia and the New Hebrides. The fact of this genus not having been recorded from Fiji or any of the groups east of the New Hebrides is very remarkable, and scarcely in accordance with the continental hypothesis. There is a persistence in type of these genera of the Coniferæ during geological time that prevents us from dealing with them on the lines that are required by the mass of the flowering-plants. Other factors intervene, and we apply with hesitation the same canons of dispersal that we employ for the general bulk of the plants of the Pacific islands. If, as often happens, a specific distinction alone separates the Conifers of the same genus on either side of the Pacific Ocean, it must possess in point of time a very different value from that which we would usually attach to specific distinctions in the floras of the Pacific islands.

DAMMARA (AGATHIS). — The Dammara region includes Eastern Australia, New Zealand, New Caledonia, with the New Hebrides, Fijian, and Santa Cruz groups, and extends north-west to Java and Borneo. Only ten species are named in the *Index Kewensis*, and of these four are assigned to New Caledonia and two to Fiji, the focus of geographical distribution being, therefore, as Seemann long since pointed out, in the islands of the Western Pacific. The absence of the genus from the neighbouring Samoan and Tongan groups is very significant; and it is evident that the ordinary agencies of dispersal, whether birds, winds, or currents, have here failed to extend the genus over a few hundred miles of sea.

When by means of observation and experiment we turn to the

fruits and look for a reply, we find in the first place that they are never to be noticed either whole or in part in the floating drift of sea or river, or amongst the stranded materials of the beaches. This is at once explained when we ascertain that the fresh cones sink in the river-water, and thus could never reach the coast in their entire condition. Nor could they do so in fragments, since the detached cone falls to pieces on the ground and the separate scales and seeds sink at once or float only for a few hours. In order to test the buoyancy of a cone after drying, it is necessary to bind it round with string to keep it from breaking down. One such fruit, after being kept for ten days, was placed in sea-water, where it floated heavily for eleven days and then sank. This is, of course, a most unnatural experiment, but it was well to have carried it out. That the entire fruit could never be transported by water is indirectly implied by Kirk respecting the fruit of Dammara australis, the Kauri Pine of New Zealand. In this case, when the fruit reaches maturity the scales, he remarks, fall away from the woody axis of the cone and the seeds are freed.

The fleshy, unprotected seeds, which, as above noted, possess little or no floating power, could scarcely withstand the injurious effect of sea-water; and they are absolutely unfitted for any known mode of dispersal by birds. It is observed by Kirk that the seeds of the New Zealand tree are widely spread by winds. But this could only avail them for local dispersion, and they appear ill-suited for being transported for more than a few paces. The seeds are winged, and are in form a little like the samara of the Maple (Acer); but they have not the same protective coverings, the wing being, however, only a little more than half the length of the entire seed. Those of both Dammara australis and D. vitiensis are about two-thirds of an inch in length, and are heavy-looking; and the agency of the wind could never be invoked except for local dispersion.

Looking at these results, the cones of Dammara may be regarded as most unsuited for any of the ordinary means of dispersal over an ocean except through the agency of man. There is, however, no necessity to introduce man's aid here, unless the gum or resin which the Fijian burns in his torches and employs as a glaze for his pottery gave his ancestors an object in carrying the cones with them in their migrations. But in that case the same argument would have to be applied to all partially useful plants, and much of the Fijian flora would lose its indigenous reputation. The endemic character of the Fijian species also militates against such a view,

and we should have to apply the same explanation to the New Zealand species, concerning which no one, so far as I know, has ever ventured to suggest that it was introduced by the Maoris.

The native names of the trees seem to have been sometimes connected with general words for gums or resins; whilst at other times the tree and the resin have separate designations. Thus the Fijians call the tree "ndakua" and the resin "makandre," which last Hazlewood in his dictionary seemingly connects with "ndrenga," the word for "gum." In my work on the Solomon Islands, page 190, I have endeavoured to show that the Maori name of "kauri" may be connected with "gatah," the general Malayan word for gums and resins, transitional stages being presented in the names of resin-yielding trees in the intermediate regions, as, for instance, by "gutur," a species of Canarium, on the Maclay coast of New Guinea, and by "katari," a species of Calophyllum, in Bougainville Straits, Solomon group. It may be pointed out that these facts of plant-nomenclature do not promise us any aid in determining the mode of dispersion of Dammara in the Western Pacific. There is a suspicious resemblance between the Fijian name of "ndakua" and "dundathu," the Queensland aboriginal name for Dammara robusta; but even if the comparison is legitimate, its explanation may lie far back in the ages in some root-word as ancient as the Malayan "gatah."

If there is a real difficulty in applying our canons of plant-dispersal to the distribution of Dammara, it is merely the same difficulty that has so often perplexed the botanist with other Coniferous genera in continental regions, such as, for instance, the occurrence of Pinus excelsa on the far-removed mountains of Europe and of the Himalayas, and the existence of the cedar in its isolated homes on the Atlas, the Lebanon mountains, and the Himalayas. Such difficulties largely disappear if we regard the present distribution of the Coniferæ as the remnant of what it was in an ancient geological period. In the case of Dammara it seems almost as idle to puzzle over its means of dispersal as to consider the mode of dispersal of the Marsupials. The questions, indeed, that affect the Dammaras of Fiji and the Western Pacific far ante-date any questions concerning a previous continental condition of those regions. The attitude of the palæobotanist to such questions would probably be one of indifference; yet to the student of plant-distribution they are of prime importance; and *nolens volens* we must admit that Dammara may well be cited

in support of any continental hypothesis affecting the Western Pacific.

PODOCARPUS.—In this connection I will mainly depend on Pilger's recent monograph on the Taxaceæ (heft 18, Engler's *Das Pflanzenreich*, 1903). More than sixty species are here enumerated, which are distributed in Africa, Asia, Australasia, and South America. With a range that extends north to Japan and south to Southern Chile in latitude 48°, this genus attains its greatest development in respect of species in Malaya, in the region comprised by Australia, New Zealand, and New Caledonia, in South America, and in Africa. Eastward of New Caledonia it is found in Fiji and in Tonga, but not in Samoa, and it is altogether absent from the Tahitian region as well as from Hawaii. Of the four species accredited by Seemann to Fiji, two are enumerated by Pilger, namely, P. affinis and P. vitiensis. The first-named, according to Stapf, is allied to P. bracteata, which occurs on the upper slopes of Kinabalu, in Borneo, and is distributed not only over Malaya, but occurs in Japan and in the Himalayas. The Tongan species, P. elatus, is, according to Hemsley, found in East Australia.

This Tongan tree is suggestive of bird-agency in the dispersal of the genus, and the same may be said of the occurrence of another species, P. ferrugineus, found in both New Caledonia and New Zealand. Since the seeds of the genus possess an outer fleshy and an inner bony covering, they would appear to be well fitted both to attract and to be dispersed by birds. In fact, we learn from Sir W. Buller that the New Zealand fruit-pigeon feeds on the seeds of the "matai" tree (Podocarpus spicata) and of the "kahikatea" (P. dacrydioides), and no doubt to the agency of frugivorous birds we can attribute the presence of the genus in Fiji and Tonga. Yet it is strange that bird-agency should have failed both with Tahiti and Hawaii. In point of size the seeds, which range from one-quarter to an inch across, present no great difficulty, and one would have thought that the birds that carried the "stones" of Elæocarpus to Hawaii could have also carried the seeds of Podocarpus.

It is, however, necessary to remember, in dealing with a genus that has a wide distribution both in time and space, that specific affinities may have a very different significance with the Gymnosperms than with most other flowering plants. When Hemsley remarks (*Introd. Chall. Bot.* p. 56) that the New Zealand Podo-

carpus spicata is closely allied to the South American P. andina, he does not imply that the two regions are in touch with each other though some 5,000 to 6,000 miles of ocean intervene. One is prepared to credit these seeds with a capacity of dispersal by birds over tracts of sea such as the extent of ocean separating New Caledonia and New Zealand, which are some 900 miles apart; but one hesitates to admit that frugivorous birds could carry them across the Southern Ocean. If we assign a home in the high latitudes of the northern hemisphere to a genus that was well represented in Europe in the Tertiary period, a movement of migration southward would explain most of the difficulties in its present distribution. The great vertical range of some of the species leads us to attribute a corresponding power of adaptation to the genus in respect of widely different climates. Thus, according to Stapf, the vertical range of P. bracteata in the Malay Archipelago extends, including varieties, from the coast to an altitude of 12,000 feet. With such a capacity for adaptation, migrations of the genus would be rendered easy over the globe.

DACRYDIUM.—It may happen that some additional light on the mystery of the Fijian Coniferæ may be afforded by Dacrydium elatum, a tree that occurs not only in Fiji, but in Further India and in Malaya. Pilger confirms Seemann's view in his identification of the Fijian tree, and this opinion is, in the main, shared by Stapf. This species, so to speak, affords us a *point d'appui* in the history of the distribution of the genus in the Western Pacific. This distribution somewhat resembles that of Dammara in extending from New Zealand (its principal centre) to Malaya and Further India; but, unlike Dammara, Dacrydium is represented in America by a solitary species in South Chile. Of the sixteen species enumerated by Pilger, seven belong to New Zealand, four to New Caledonia, three to Malaya, one to Tasmania, and one to Chile. The seeds are, as a rule, smaller than those of Podocarpus, and on account of their somewhat similar structure would serve as bird-food, and might be distributed in this fashion. Yet the genus has been only recorded from Fiji, and is not only unrepresented in Hawaii and Tahiti, but is also not known from the Tongan and Samoan groups that belong to the Fijian floral region of the Pacific. Capacities for dispersal appear meaningless here, especially when we have regard to the solitary American species, Dacrydium fonkii, that as a shrub finds a refuge in the bleak region of Southern Chile.

The three Fijian genera of the Coniferæ, Dammara, Podocarpus, and Dacrydium, appear at first sight to be beyond the reach of our canons of plant-dispersal, by which we connect specific affinity with a continuity of range, and by which we co-ordinate means of dispersal and area of distribution. We begin to realise that there may have been an age of Coniferæ in the Pacific islands that is even less amenable to our methods than the later era of the Compositæ and Lobeliaceæ in Hawaii and Tahiti. Such an age would be concerned only with that region in the Western Pacific which is now held by the genera Dammara, Podocarpus, and Dacrydium, a region that did not participate in the era of the Compositæ and Lobeliaceæ. We thus have evidence of an ancient era of the Coniferæ that was confined to the Western Pacific, and of a later era indicated by the peculiar genera of Compositæ and Lobeliaceæ that was restricted to Hawaii and to Eastern Polynesia (Tahiti, Rarotonga, &c.). The key to the situation here presented seems to lie in the following considerations.

It is assumed that there was an age of Coniferæ in the Pacific, or rather that this region shared in an era of dispersion of existing genera of the order. In this age only the islands of the Western Pacific participated, neither the Hawaiian nor the Tahitian islands taking a part in it. Such a result is to be attributed either to the inability of these genera of Conifers to reach Hawaii and the islands of East Polynesia, or to the non-existence of the Hawaiian and Tahitian archipelagoes at that epoch. The first explanation seems scarcely acceptable, since, although the powers of dispersal of the genus Dammara are very limited, there seems no reason why the genera Podocarpus and Dacrydium could not have reached those distant regions of the Pacific. The second explanation is most probable, and it is the one suggested by Hillebrand (p. xxx) in the case of Hawaii, namely, that "the absence of Gymnosperms militates for the view that the islands were formed subsequent to the age in which these were universally distributed."

If this conclusion is legitimate we have here a datum-mark in the history of the islands of this ocean. Before the appearance of the Hawaiian and Tahitian islands (using the term Tahitian to cover the East Polynesian region) there existed a land-area in the Western Pacific held by the Coniferæ, probably in the late Secondary period. After the formation of the Hawaiian and Tahitian islands, perhaps in the early Tertiary epoch, came the age characterised by the ancestors of the present endemic genera

of the Compositæ and Lobeliaceæ, and of a few other orders in Hawaii and Tahiti. In this age the islands of the Western Pacific do not seem to have participated, and it is to be inferred that this was an age of extensive but probably not of complete submergence in that part of the ocean, since at least the genus Dammara was able in places to hold its ground. Then ensued the great Tertiary emergence of the land-areas of the Western Pacific, when small islands that dotted the sea-surface in this region became the nuclei for the formation of the large islands of the present Fijian, New Hebrides, and Solomon groups. This prepared the way for the migration of Malayan plants which now predominate over the islands of the tropical Pacific; and in a later age man, following the same track from Indo-Malaya, occupied these islands.

In my volume on the geology of Vanua Levu it was shown that the Tertiary period was an age of submergence in the Western Pacific, and a disbelief in any previous continental condition was expressed. My later view is more in accordance with that of Wichmann, who, on geological grounds, contended that the islands of the Western Pacific were in a continental condition during the Palæozoic and Mesozoic periods, and that their submergence and subsequent emergence took place in Tertiary times. The distribution of the genus Dammara has thus led me to modify the views expressed in the final chapter of my first volume on the geology of Vanua Levu. Though still holding that there is no geological evidence that the various islands of the Fijian group were ever amalgamated, or that they were joined as such to the westward groups, it is quite possible that their position was indicated by a few small islands a few miles across and a few hundred feet in height in early Tertiary times. On these small islands, which probably represented the remains of a submerged Mesozoic land-area, such as is in part implied in Dr. Forbes' *Antipodea*, or in Mr. Hedley's *Melanesian Plateau*, the genus Dammara survived. Such islands merely indicated the situation of some of the present groups of the Western Pacific, which have been since largely built up by submarine eruptions, and the greater number of the islands were no doubt completely submerged. Between the groups as we know them now there never was any land connection, since they are the product of later eruptions, mainly submarine; and they have acquired their present composite character during the emergence that followed the period of volcanic activity. Except, perhaps, in New Caledonia, which does not seem to have shared in the Tertiary submergence, the islands of the Western Pacific have

a configuration acquired in comparatively recent times, and one that gives no idea of the character of the Mesozoic continent.

Such, as I understand them, are the indications of the Fijian Coniferæ and particularly of Dammara. In the distribution of this genus we have outlined an ancient, more or less continuous land area which, with the exception of a few isolated points, disappeared beneath the sea in Tertiary times to re-appear near the close of that period in the form of a number of archipelagoes that were largely built up by submarine eruptions, and probably altogether mask the form of the original land-area. It may be remarked that New Zealand, which largely shared in the Tertiary submergence, especially in the Miocene age, is included in the range of the genus Dammara, as well as in those of the genera Podocarpus and Dacrydium.

Summary.

(1) The evidences of a mountain-flora in Tahiti, as indicated by the non-endemic genera, though, as we would expect, of a scanty nature when contrasted with Hawaii, are nevertheless of considerable interest. There is much kinship with the Hawaiian mountain-flora, but it is mainly confined to genera from high southern latitudes, such as Nertera, Coprosma, Cyathodes, and Astelia, which are all dispersed by frugivorous birds. Amongst other plants linking the Tahitian mountains with the region of the Antarctic flora, and with New Zealand in particular, may be mentioned Coriaria ruscifolia and the genus Weinmannia.

(2) On account of their relatively low altitude the Fijian islands do not present the conditions for an alpine flora. Traces, however, of the Antarctic flora, or of the New Zealand flora, occur on occasional mountain-tops, as is indicated by the occurrence of species of Lagenophora, Coprosma, and Astelia. In Samoa the mountain-flora is also scantily developed, as we might have expected; but here occurs the genus Vaccinium as well as a widely-ranging species of the Antarctic flora, Nertera depressa.

(3) The route by which some of the representatives of the flora of high southern latitudes reached the mountains of the islands of the tropical Pacific is directly indicated by the genus Coprosma to have been from New Zealand by way of the Kermadec Islands.

(4) In the distribution of plants possessing drupes or berries that connect the tropical islands of the South Pacific with New Zealand, it is highly probable that birds of the genus Porphyrio

(Swamp-Hens or Purple Water-Hens) have taken a prominent part.

(5) In the possession of species of the three genera of Coniferæ, Dammara, Podocarpus, and Dacrydium, which often largely form the forests of the mountain-slopes, Fiji is distinguished from all the other groups of the open Pacific with the exception of Tonga, which owns a species of Podocarpus probably introduced by birds. From the circumstance that Dammara has no known means of crossing a tract of ocean, whilst Podocarpus and Dacrydium could be dispersed by frugivorous birds, all three genera having, however, much the same limited distribution in the Western Pacific, it is apparent that something more than a question of means of dispersal is here involved. It is assumed that they mark the site of a Mesozoic continental area in this region, and that at this period the Tahitian and Hawaiian groups which possess no Conifers did not exist. This area was submerged during the Tertiary period with the exception of a few peaks that formed small islands on which the Conifers held their ground. During the Tertiary submergence of the Western Pacific region, the Hawaiian and Tahitian islands were built up by subaërial volcanoes and received the ancestors of the Compositæ and Lobeliaceæ that now exist as endemic genera in those groups. Then followed the emergence of the islands of the Western Pacific and their occupation mainly by Indo-Malayan plants that extended eastward over the Pacific. Thus in the Pacific there has been first an age of Conifers in which the islands of the Hawaiian and Tahitian regions could not participate, since they did not exist. Then ensued an era of American forms of Compositæ and Lobeliaceæ in which only Hawaii and Tahiti participated, since the Western Pacific region was submerged. Lastly came the invasion of Indo-Malayan plants, which have largely occupied every group in the tropical Pacific.

CHAPTER XXV

THE ERA OF THE NON-ENDEMIC GENERA OF FLOWERING PLANTS (*continued*)

THE AGE OF THE MALAYAN PLANTS AS REPRESENTED IN THE LOW-LEVEL FLORA OF HAWAII AND IN THE BULK OF THE FLORAS OF THE FIJIAN AND TAHITIAN REGIONS

The Age of Wide Dispersal over the Tropical Pacific.

The widely dispersed genera which possess only peculiar species in Hawaii. — Pittosporum. — Reynoldsia. — Gardenia. — Psychotria. — Cyrtandra — Freycinetia.—Sapindus.—Phyllanthus.—Pritchardia.—Summary.

WE pass now from the consideration of the mountain-flora of Hawaii and its scanty representation in the Fijian and Tahitian regions to a discussion of the low-level Hawaiian flora, belonging to stations under 4,000 or 5,000 feet, and of the corresponding floras of the other two regions. It has been previously pointed out that in mass the plants of Fiji and Tahiti correspond to the low-level flora of Hawaii.

There are numerous ways of comparing this era of the non-endemic genera of these three regions of the Pacific. The necessities of space, however, compel me to treat the subject only in an illustrative fashion, and in adopting the plan which seems easiest and simplest I have also been obliged to keep my limitations mainly in view.

THE WIDELY-DISPERSED GENERA WHICH POSSESS ONLY PECULIAR SPECIES IN HAWAII.

Amongst the oldest denizens of the Pacific islands in this era of the non-endemic genera may be taken those genera of flowering plants which are found in all three regions, Hawaii, Fiji, and

Tahiti, but possess in the first group only endemic species, whilst in the other two regions they may include species both confined to and occurring outside the respective groups. They represent an age of wide dispersal over the Pacific, an age which for Hawaii has long since passed away, since all the genera have been disconnected from the outer world, whilst in the groups of the South Pacific they as a rule in each case remain in touch through some of the species with the groups around.

The problem of plant-distribution in the Pacific thus assumes a different aspect in an age which we term Malayan or Indo-Malayan, since the bulk of the plants are thence derived. The earliest age of the Coniferæ was, as we have seen in the previous chapter, restricted to the region of the Western Pacific. The following age of the Compositæ and the Lobeliaceæ was concerned with the regions of Tahiti and Hawaii. Now, however, in the Malayan era, the whole of the tropical Pacific is concerned. Yet, although we shall still regard, for purposes of convenience, the groups of Fiji, Tahiti, and Hawaii as the three foci of plant-distribution, it will soon become apparent that in future there will be in reality only two regions to deal with, the Hawaiian in the North Pacific, and the whole region of the South Pacific extending from Fiji to Tahiti and as far east as the islands stretch. It will be also seen that in making our comparison we shall sometimes have to regard each of the principal Hawaiian islands as the equivalent as a plant-centre of an entire archipelago of the South Pacific.

The genera that are here selected to represent this epoch of wide dispersion are very characteristic of the floras of the Pacific islands. Genera like Pittosporum, Gardenia, Psychotria, Cyrtandra, Freycinetia, and others one meets with everywhere in the larger islands, and it should be observed that they are predominantly Old World, and more especially Malayan, in their origin, not a single purely American genus, unless we except the decadent genus of fan-palms, Pritchardia, occurring among them. Here we notice [what we shall see is especially typical of the era of the non-endemic genera, excepting those of the lofty uplands of Hawaii] that the frugivorous bird has been the principal agent in dispersing the plants, quite two-thirds of the total genera possessing drupes or berries that would attract such birds. The transport of seeds or seedvessels in birds' plumage, which was a conspicuous feature in the case of the mountain-flora of Hawaii, is not a feature of this age of wide dispersal of tropical plants over the Pacific.

The genera selected to represent this age are given in the following table. Those on which my observations directly bear, or in which I was particularly interested when in the Pacific, will be discussed in detail from the standpoint of dispersal; whilst only a brief reference will be made to a few of the others, not, however, from lack of materials at my disposal, but merely to keep this volume within moderate bounds.

Genera selected to represent the Age of Wide-dispersal of Indo-Malayan or Malayan Plants over the Pacific, and possessing in Hawaii only Endemic Species.—Most of the genera of this age are exclusively from the tropics of the Old World, whilst those found on both sides of the Pacific can be shown in most cases to have been derived from the same source, and only very few, like Pritchardia, can be traced to America.

Pittosporum (Pittosporeæ).
Sapindus (Sapindaceæ).
Reynoldsia or Trevesia (Araliaceæ)
Gardenia (Rubiaceæ).
Psychotria (Rubiaceæ).
Cyrtandra (Gesneraceæ).
Phyllanthus (Euphorbiaceæ).
Pritchardia (Palmaceæ).
Freycinetia (Pandanaceæ).

PITTOSPORUM (Pittosporeæ).

This genus, which contains nearly a hundred species, usually of small trees, is widely spread in the warmer regions of Africa, Asia, Australia, and New Zealand. It is also especially a genus of oceanic islands, occurring not only in those of the Pacific but also in Madeira and Teneriffe in the Atlantic.

Though found in most of the larger Pacific groups, it has apparently never been recorded from Samoa. From Hawaii ten species are known, all peculiar to that group. About half a dozen have been described from Fiji, of which three at least have been observed outside the group in the neighbouring Tongan Islands. Rarotonga possesses a peculiar species which, however, is so near to two other Fijian and Tongan species that, according to Cheeseman's memoir, they may have to be subsequently united. Tahiti is credited by Drake del Castillo with a solitary species

widely distributed in the Old World, whilst in the *Index Kewensis* a peculiar species is assigned to it. They form small trees of the wooded mountain-slopes of Fiji; whilst in Hawaii, beside occurring in the lower forests, they may extend to altitudes of between 5,000 and 7,000 feet. In the connection that more or less exists between the species of the South Pacific archipelagoes, and in the endemic character of all the Hawaiian species, we see the principle exemplified that there are two regions of distribution in the islands of the tropical Pacific—the Hawaiian region and the South Pacific region.

Before their dehiscence, the wrinkled, woody capsules would seem very unlikely to attract birds; but the observer on handling an opening fruit, with its orange or brightly coloured lining and displaying black or dark-purple seeds immersed in a semi-liquid pulp, would form a different idea of the plant's capacity for this mode of dispersal. The mature dehiscing fruits are very conspicuous on the tree; and the seeds covered with the "sticky" material of the pulp might possibly adhere to birds pecking at the fruit. But this would only aid in local dispersion, since the weight and size of the seeds, 5 to 8 millimetres ($\frac{2}{10}$ to $\frac{3}{10}$ inch), would unfit them for this mode of transport across an ocean. They are, however, sufficiently protected by their hard tests to be able to pass unharmed through a bird's intestinal canal.

Yet the distribution of the species of Pittosporum in the Pacific would show that their dispersal is more a matter of the past than of the present. Out of the ten peculiar Hawaiian species, Hillebrand designates none as generally distributed over the group. But it is evident that, though it is on the point of breaking off, some sort of connection still exists in the South Pacific between the Tongan and Fijian species, and until recently between the species of those two groups and of Rarotonga.

REYNOLDSIA (Araliaceæ).

The Polynesian genus of Reynoldsia, originally established by Gray, is merged by Hooker and Bentham into the Malayan genus Trevesia, a step that brings the Pacific plants into line with many other of the plants hailing originally from the Old World. The significant fact in the distribution of this genus of small trees in the Pacific is that its dispersal over the ocean has ceased long ago, since the three species here occurring are restricted each to a particular group, namely, to Hawaii, Tahiti, and Samoa. Yet the

inter-island dispersal still continues in the Hawaiian Group, the species characteristic of that archipelago being found in all the islands.

Reynoldsia sandwicensis came frequently under my notice in Hawaii, and the fairly fleshy drupes, about one-third of an inch, or 8 millimetres, in size, with their crustaceous pyrenes appeared to me well fitted for assisting the dispersal of the plant by frugivorous birds. Yet here the same question arises that presents itself with so many other Hawaiian plants, and that is, How has it happened that the birds have continued to disperse the species over the scattered islands of this group long after they ceased to transport fresh seeds from the outside world? The answer is an obvious one. The birds that originally brought the seeds of the parent species from some distant region came at last to remain permanently in the Hawaiian Group, and not only the plant but probably also the bird has since undergone specific differentiation. This link between bird and plant in the floral history of a group of Pacific islands is the common theme of the story of most of the endemic species of plants in this region of the globe.

GARDENIA (Rubiaceæ).

This genus, comprising about a hundred known species, is spread over tropical Africa, Asia, and America, and over all the groups of the tropical Pacific. On account of their handsome, white, scented flowers these shrubs are much appreciated by the Pacific islanders, who employ the flowers for personal decoration. Some ten species have been described from the groups of the open Pacific, all of which, with the exception of Gardenia tahitensis, which ranges the South Pacific from Fiji to the Marquesas and Tahiti, are seemingly peculiar to the different archipelagoes. Thus there are some six species endemic to Fiji, one to Samoa, and two to Hawaii.

The Hawaiian Islands are, however, quite isolated in this respect, since the group possesses only peculiar species; whilst a solitary species keeps up the connection between the groups on the south side of the equator. The Gardenias thus tell the same story of complete isolation in Hawaii, and of partial isolation in the archipelagoes of the South Pacific that is repeated by many other Pacific genera. Yet in Hawaii there has subsequently been some inter-island dispersal, since the species are not restricted each to a single island, but are found on two or three islands. The

significance of the relation of the Hawaiian Gardenias to those of the combined Fijian and Tahitian areas consists in regarding the two regions, the Hawaiian and the South Pacific, as of equivalent value, and each large Hawaiian island as equivalent to one of the southern archipelagoes.

The Station of the Pacific Gardenias.—Although they may occur in the forests, the Gardenias of the Pacific are most characteristic of dry, thinly vegetated localities, and they have an inclination for the vicinity of the coast. In the Tahitian Group, as we learn from the writings of Nadeaud and Drake del Castillo, Gardenia tahitensis thrives much better on coral islands than on volcanic soils, and, in fact, rarely quits the "*région madréporique.*" It is sometimes planted in Polynesia near the houses, and both Nadeaud in Tahiti and Cheeseman in Rarotonga consider that it was probably introduced into those islands before the arrival of Europeans. The aborigines may have assisted in the dispersal of the genus to a small extent, but from the presence of peculiar species in Hawaii, Samoa, and Fiji it is apparent that the genus is truly indigenous in the Pacific islands, and long antedated their occupation by man. This is also evident from the station of the species in Hawaii, Samoa, and Fiji. In Hawaii they may be found on the dry forehills in the vicinity of the sea-border. In Samoa, as Reinecke informs us, Gardenia tahitensis is very widely spread in the mountain-forests, whilst the endemic species is found thriving in inundated coast districts. In Fiji I found the Gardenias to be especially characteristic (as is also pointed out by Horne) of the dry districts on the leeward side of the larger islands. On the rolling "talasinga" or "sun-burnt" plains of the north side of Vanua Levu they thrive in numbers; and here their leaf-buds and the extremities of the young shoots are often tipped or covered over with an amber-like gum-resin which the natives chew.

The Mode of Dispersal of the Pacific Gardenias.—The fruits of this genus are usually described as indehiscent. If this were true of Pacific plants it would be very difficult to explain the dispersal of hard, dry fruits an inch in size over this region. In the case of two or three Fijian species, I paid especial attention to this point by examining the plants in fruit. As exhibited in Fiji the fruits are globose, hard, and almost stony, with persistent adherent calyx, the seeds lying horizontally in a pulp at first firm and subsequently softening as the fruit matures. The fruits are not as a rule to be observed opening on the plant; but they are to be seen dehiscing septicidally on the ground beneath, the detached woody

valves being scattered around. If one of the fruits gathered from the plant is kept soaking in water for some time it will begin to dehisce; and this is probably what occurs with fallen fruits in wet weather. Dr. Hillebrand regards the fruits of the Hawaiian species as indehiscent. I did not myself examine them, but it is not improbable that, like those in Fiji, they dehisce whilst lying soaking on the ground.

Judged merely from the dispersal standpoint, the fruits of the Fijian Gardenias come near to those of Pittosporum, and both can be in a sense described as baccate capsules. The flat, crustaceous seeds of Gardenia, which are usually two or three millimetres in size, are also well fitted for passing without injury through the digestive canal of a bird. It is likely that the two genera have been dispersed in the Pacific by the same kind of birds; and it should be remarked that their distribution is somewhat similar, both belonging to the warm regions of the Old World.

It might at first appear from some experiments of mine made in Fiji that the dried fruits of Gardenia could be dispersed over oceans by the currents. This receives some support by the preference for a littoral station sometimes shown by G. tahitensis in Tahiti, and by the occurrence of G. zanguebarica in the East African strand-flora (Schimper's *Ind. Mal. Strand-flora*, p. 131). It will, however, be pointed out that currents could only have aided the dispersal of the genus to a limited extent. The fresh fruits of Fijian species, with or without the adherent calyx, have little or no buoyancy, and the seeds sink even after drying for months. But it was ascertained that fruits which had been kept for three months floated after four or five weeks' immersion in sea-water. On examination, however, it was found that the valves gaped a little, being only held in apposition by the adherent calyx, and that water had penetrated into the interior, the pulp being in a state of decay. The fruits were, in fact, kept afloat in the latter part of the experiment partly by the investing calyx and partly by gas generated in the decomposing pulp. Ultimately they broke down altogether and the seeds sank. In the "rough-and-tumble" of ocean-transport this could scarcely be deemed an effective means of dispersal; and in the open sea a fortnight would probably represent the limit of the floating power. It is to the agency that has distributed the genus Pittosporum over the Pacific that we must look for the explanation of the dispersal of Gardenia over the same ocean, namely, to birds.

PSYCHOTRIA (Rubiaceæ).

We find in this large genus of the Old and New Worlds a typical example of the plants with fleshy drupes containing hard pyrenes that represent, from the standpoint of dispersal, a common Rubiaceous type of plant in the tropical Pacific. Such plants, of which those of Coprosma and Nertera may be cited as other instances, are in a generic sense always widely distributed in these islands. They are eminently suited for dispersal by frugivorous birds; and it is a matter for surprise, therefore, that in a genus like Nertera the solitary Pacific species has such a wide range, whilst with Psychotria and Coprosma the numerous species are usually restricted to particular groups. Genera doubtless have their periods of development and decadence in the Pacific, and probably Nertera is to be regarded as a decadent genus. These Rubiaceous genera, however, appear to be well fitted for the investigation of the centres of dispersal of particular genera and of their relative age.

The Psychotrias in these islands are typically shrubs of the shady woods, and they may be seen thriving best where the forest-growth is rank and the humidity greatest. Their bright red ovoid drupes, which range from eight to twenty-five millimetres in length ($\frac{1}{3}$ to 1 inch), would readily attract birds, and their crustaceous pyrenes, that vary between five and eight millimetres ($\frac{1}{5}$ to $\frac{1}{3}$ inch) in length, would pass unharmed through a bird's digestive canal. That fruit pigeons can distribute their seeds over the Pacific has been long established, and Mr. Hemsley includes Psychotria amongst those genera which, from the collections of fruits and seeds found in the crops of fruit-pigeons, made by Professor Moseley, myself, and others, in the groups of the Western Pacific, are "known to be dispersed by birds in Polynesia" (*Introd. Bot. Chall. Exped.*, p. 45). It is thus hardly necessary to point out that neither the entire fruits nor the separate pyrenes could be transported by the currents, my observations showing that in both cases they sink at once or in a day or two.

Psychotria, however, is an enormous genus including, according to the *Index Kewensis*, some 600 or 700 described species, distributed in the tropics all over the world, and also extending into subtropical regions, the greatest concentration being in America. It is described in the *Genera Plantarum* as a polymorphous genus distinguished by no certain characters from some other genera of

the tribe of the Rubiaceæ to which it has given its name. We have here a genus that has overrun the tropical regions of the world, probably originating in America; and we may contrast it with the relatively small Rubiaceous genus of Coprosma (with its three score of species, and quite comparable with it from the standpoint of capacity for dispersal), that, having its birthplace in New Zealand, is only beginning to reach the mainlands of the New and the Old World.

One is a genus of the tropics and the other is a genus of south temperate latitudes; and both have occupied the Pacific islands; but Coprosma naturally finds its most appropriate station on the cool uplands of Hawaii and Tahiti. We may ask, indeed, whether the great contrast in the fecundity of the two genera, dispersed as they are in the same fashion by the agency of frugivorous birds, is to be connected with questions of relative antiquity or with geographical position. It would certainly have been a more difficult task in the past, other things being similar, for a New Zealand genus to stock the temperate regions with its species than for a tropical American genus to overrun the warmer regions of the globe. However that may be, the age of dispersal of both genera is largely over now.

A vast genus like Psychotria, that is not sharply defined from other genera, presents difficulties to the systematic botanist which are reflected in a complex synonymy; but there are certain broad facts which the student of dispersal can gather for himself without much difficulty. When we look at its distribution in the islands of the open Pacific, we find that the genus attains its greatest development in the Western Pacific, there being from thirty to forty species known from Fiji and quite a dozen from Samoa, and that it shades away as we proceed eastward and northward, some six species being recorded from Tahiti and the Marquesas, two from Hawaii, and one from Juan Fernandez near the South American mainland. The arrangement of the species shows fairly conclusively that the genus Psychotria, as it is found in the Pacific, has, like most of the other plants of this era of non-endemic genera, been derived from the Asiatic side of the ocean. (The absence of species of this genus from Mr. Cheeseman's Rarotongan collections seems strange. It is represented by some species in Tonga, and it is extremely probable that it will be subsequently found also in the Rarotongan group.)

That the age of dispersal of the genus Psychotria over the Pacific islands has almost passed away is evident from the circumstance that

of the half-hundred species known from these groups, all but some four or five are confined to particular groups. There is one species, P. insularum, that ranges over the South Pacific from Fiji to the Tahitian region; and there are two or three others that keep up a connection between the adjacent groups of Fiji, Samoa, and Tonga, the last having no peculiar species; but, apart from these indications, isolating influences generally prevail. The two Hawaiian species are both endemic and are only recorded from the island of Kauai, so that in that archipelago there has not even been inter-island dispersal of the genus. For Fiji it would seem from the *Index Kewensis* and other authorities that at least two-thirds of the species are confined to the group. Of the dozen Samoan species only two or three are known outside the islands. Four out of the five Tahitian species are peculiar, and the only Marquesan species named by Drake del Castello is endemic. Even the solitary species of Juan Fernandez is endemic, there attaining the dimensions of a fair-sized tree. It forms the subject of an illustration in Schimper's *Plant-Geography*, page 491.

Speaking generally, birds may be said to have almost ceased dispersing this genus over the Pacific. This is not because birds have ceased to be partial to the fruits, but because the frugivorous birds that used to range over the Pacific archipelagoes now restrict their wanderings to the limits of a single group. If we find occasionally in other parts of the world, as in the occurrence of a Florida species of Psychotria in the Bermudas, some evidence of a dispersal still in operation, this is nothing more than we observe in the case of a few of the Polynesian species now. The connection between birds and plants in the Pacific is discussed in Chapter XXXIII. In this ocean the dispersal of the genus is now practically dead, and Psychotria presents no exception to that general tendency towards isolation and differentiation exhibited by most genera of the tropical Pacific as the result of failure of the means of dispersal.

CYRTANDRA (Gesneraceæ).

This remarkable genus of shrubs, which forms the subject of an important memoir by Mr. C. B. Clarke (*De Cand. Mon. Phan.* v. 1883–87), offers, as Mr. Hemsley remarks, an example of a Malayan genus extending to Polynesia and there developing numerous species. Of some 180 known species, about 80 or nearly half are confined to Polynesia, the rest being mainly Malayan. Of the

Polynesian species about thirty are Hawaiian, twenty Fijian, fifteen Samoan, and twelve Tahitian ; whilst solitary species are restricted to Tonga and Rarotonga respectively.

The most significant feature in the distribution of this genus in Polynesia is not only, as is pointed out by Mr. Clarke, that every group has its peculiar species, but that very few species are found in more than one group, and that even in the same archipelago each island has its own species. Thus, of the thirty Hawaiian species, all of which are peculiar to the group, only two or three, according to Hillebrand, are at all generally distributed over the islands, whilst four-fifths have not yet been found to be common to more than one island. So again, all the species found in the Tahitian Group proper are peculiar, with the exception of one extending to the neighbouring Paumotu Islands ; and even Rarotonga has its own species. In the region comprising Fiji, Tonga, and Samoa the same rule prevails, only two or three species connecting the three groups together. There thus seems to be not only a complete suspension of the dispersal agencies between the various archipelagoes, but also often between the several islands of a group. This is particularly to be remarked with the relatively contiguous groups of Fiji, Samoa, and Tonga, since with most other genera a number of species are common to all three archipelagoes. "The polymorphism of the Hawaiian Cyrtandras," says Hillebrand, "is extraordinary : no single form extends over the whole group, and not many are common to more than one island. The variations affect nearly every part of the plant, and branch out and intercross each other to such an extent that it is next to impossible to define exact limits of species." Genera, however, run riot in other groups of the Pacific besides Hawaii, and Reinecke uses much the same language with reference to Elatostema, an Urticaceous genus in Samoa, attributing the wealth of forms to the sensitiveness of the plants to the varying conditions of station (see Chapter XXVII).

The behaviour of Cyrtandra in the Pacific is rather startling to the student of plant-dispersal when he reflects on the suitability of the berries for dispersing the plant through the agency of birds. That the vegetation of oceanic islands should be of an endemic character is a fact, remarks Mr. Clarke, that is illustrated by many other orders besides the Gesneraceæ. But the point we have to remember is that not only does the genus Cyrtandra display the same prolific character in the large continental islands of Malaya, such as Java, Sumatra, and Borneo, each of which possesses at least a couple of dozen species, but that this seems to be a feature of the

tribe Cyrtandreæ and of the whole order. The genera, as observed by Mr. Clarke, are very continuous in their areas of distribution, and in the tribe Cyrtandreæ there are very few species that extend to more than one region, whether on the mainland or in an oceanic archipelago. In the Himalayas, he says, closely allied species of Didymocarpus are confined to single districts, although there appears no reason either in soil or climate why they should not spread to the adjacent valleys.

There is therefore, we may infer, nothing peculiarly characteristic of insular floras in this prolific display of the genus Cyrtandra in the Pacific, except that it is rather more pronounced in an oceanic group than in a continent. The same general cause is working alike in an island in mid-ocean, in a large continental island bordering the mainland, and on the mainland itself. With the Pacific Cyrtandras as with the British species of Rubus the variability may be so great that the ordinary agencies of dispersal fail to keep it in check; and when, as in the Pacific islands, the suspension of the activity of these agencies is complete, the formative energy of the species knows no bounds other than the determining limits of station. Our lesson from the Pacific Cyrtandras is therefore this. The isolation of the oceanic archipelagoes may not explain the endemic character of the flora, but only the extreme degree to which the endemism is carried. When a genus is in its prime, it can defy all the limiting conditions imposed by similarity of station and by free and unchecked means of dispersal, the essential marks of a species or a genus having probably in their development little or no connection with environment.

The Cyrtandras of the Pacific Islands are most frequent where vegetation is rank, as in moist woods, in humid valleys, and in shady ravines and gorges; but they may also occur in more exposed and drier stations. They often grow gregariously, and Schimper says the same of them in the Java forests (*Plant-Geography*, pp. 291, 297).

The fruit of the genus is described by Clarke as a fleshy or a coriaceous berry. Almost everywhere in the Pacific groups the berry is white and fleshy; but it is noteworthy that out of the nine Tahitian species where the fruit is particularised by Drake del Castello, in two cases it is designated a capsule and in seven a berry. It is in this connection worth remarking that in Malaya other genera of the tribe often have capsular or dry and coriaceous berries. The conspicuous white berries of the Pacific species would

readily attract birds, and their minute roughened seeds scattered through the pulp might readily adhere to their plumage or even be ejected unharmed in their droppings. As respecting the capacity for dispersal, the Pacific Cyrtandras come near the Hawaiian endemic genera of Lobeliaceæ with baccate fruits and minute seeds. Speaking of Malayan genera of the tribe Cyrtandreæ, Mr. Ridley says that their dry, dull-coloured, and inconspicuous corky fruits are often devoured by animals. The seeds, on account of their roughened surface, adhere to rocks and other surfaces and readily germinate.

FREYCINETIA (Pandanaceæ).

If there is any genus of tropical plants to which the student of distribution can look for guidance in the region of the Pacific, it is to Freycinetia as dealt with by Dr. Warburg in his monograph on the order (Engler's *Pflanzenreich*, iv. 9, 1900). Its characters and its distribution are well defined ; and here, if anywhere, we might be able to work out the history of a genus. In the words of the German botanist, it stands quite apart from Pandanus and Saranga, the two other genera of the order. When Hillebrand was preparing his work on the Hawaiian flora, more than a quarter of a century ago, only about thirty species were known. Warburg's list, excluding doubtful forms, comprises sixty species, and even this number the author surmises will be doubled in future years. The later investigators, however, have not materially extended the range of the genus ; and the statement of the botanists of a generation ago, that it extends from Ceylon through Malaya and Australia to New Zealand, and is found on almost every elevated island of the Pacific, can only be supplemented by extending its area to the Asiatic mainland in Burma where a wide-ranging Malayan species exists.

It is, however, remarkable that no endemic species can be with certainty accredited to the mainland of Asia either in Burma or in the Malay peninsula where the genus also occurs. The Malayan region from Java to the Philippines possesses quite three-fifths of the species, and it is singular how few wide-ranging species there are. The Philippine Islands, Borneo, Celebes, Sumatra, Java, New Guinea, &c., have all their own species, the only wide-ranging plant being Freycinetia angustifolia, which occupies the region from Burma to Java and Borneo. So also in the Pacific, there is no widely distributed species, every group possessing its own plant or plants, and there does not appear to be any Freycinetia that is

common to two groups. Thus, Hawaii and Tahiti each have their own species. Rarotonga, according to Cheeseman, owns a peculiar but not yet fully described form. Samoa has two and Tonga has one species. Westward from Tonga and Samoa the numbers of species increase, Fiji possessing five and New Caledonia four. Australia and New Zealand each claim two species as their own.

Dr. Warburg, who has studied the genus in its home, remarks on page 43 that none of the species possess any means of dispersal enabling them to cross an ocean; and he connects with this the fact that the genus is only found (to use his own words) on islands like those of Samoa, Tahiti, and Hawaii, that possess a "palæobiotic" nucleus (*paläobiotischen Kern*), and not on islands like the Bonin Islands of new formation (*auf Neubildungen*). This attitude towards the problem of plant-distribution in the Pacific is backed by a great experience; but it is one, of course, that is directly opposed to the line of argument followed in these pages; and it is needless to say that it is not encouraging to the student of plant-dispersal. Yet one could hardly look upon the islands of the Tongan Group with their representative of the endemic Freycinetias as of more ancient origin than the Bonin Islands that have none; and plants that find their homes on the peaks and in the forests of mountainous islands would rarely find a suitable station on the low coral islands of the Pacific. It is, however, noteworthy that Professor Schimper is inclined to include a species of Freycinetia as amongst the strand-flora of the coral islands of the Java Sea (*Ind. Mal. Strand-flora*, p. 134). With regard to the question of the means of dispersal of Freycinetias, it will at once be shown that these plants possess many opportunities for dispersal by birds.

Though in our own time dispersal by birds between the various Pacific archipelagoes is often largely suspended, the inter-island dispersal in each group is usually active through the agency of birds, now like the plants they distribute confined to each group. Thus with Freycinetia we find that, notwithstanding that each Pacific group is, as regards this genus, isolated from the others, the separate islands, as in the case of those of Hawaii, may possess a common species dispersed over the area. The ripe fruit, which consists of a number of berries in a head or spike, is juicy and pulpy, and contains in each berry a large number of minute oblong or fusiform seeds, usually one or two millimetres long and possessing thick toughish tests. Birds, indeed, are fond of pecking at the ripe fruit-heads in Hawaii. Thus we learn from the *Aves Hawaiienses*

of Wilson and Evans that a Grosbeak (Psittacirostra) and the Hawaiian Crow (Corvus tropicus) feed principally on ripe Freycinetia fruits, the seeds having been often found by Mr. Wilson in the stomach of the former bird. No doubt these birds distribute the seeds over the islands of the group. Mr. Perkins tells me that the Grosbeak is found unmodified all over the group, and that it no doubt frequently gets carried *nolens volens* from one island to another. In his memoir on the birds in the *Fauna Hawaiiensis*, he remarks that the essential food of the "Ou," the native name of this bird, is the fruiting inflorescence of Freycinetias. The "Oo" (Acrulocercus) and the Hawaiian Crow above mentioned, as he also observes, feed on these ripe red fruits. Like Mr. Wilson, he sometimes found the Crow absolutely filled with this food to the exclusion of all others (see Chapter XXXIII). Facts of a similar kind came under my notice whilst in these islands. Thus on one occasion I observed, on a leaf below a fruit-head that had been partly eaten by a bird, a pellet half an inch long composed entirely of Freycinetia seeds well soaked with the gastric juices and apparently only recently disgorged. Sir W. Buller refers to different New Zealand birds, as the Banded Rail (Rallus philippensis), the Kaka Parrot (Nestor meridionalis), and the "Tui" (Prosthemadera), that live on the "sugary flowering spadices" of Freycinetia Banksii. One can legitimately suppose that they also attack the juicy berries. It is singular that as we learn from Dr. Warburg (p. 17), Flying-Foxes (Pteropidæ) feed on the flowers and top-leaves of many species of Freycinetia, and he considers that they would aid in fertilisation by carrying about the pollen in the hair of the head. Here again it would seem to us highly probable that whilst brushing past a ripe fruit-head these bats might readily carry away in their fur some of the minute seeds, which in the fresh berry are "sticky" or adhesive.

Just as it was possible in the case of Coprosma in the South Pacific (see page 296) to connect its distribution with the range of the Purple Water-Hens (Porphyrio), so it may perhaps be legitimate to associate the range of Freycinetia over Polynesia with the distribution of the Honey-Eaters (Meliphagidæ) in the Pacific, a family sometimes possessing peculiar genera as in New Zealand and Hawaii, and one in which the species have usually a very confined range, being sometimes limited to a single island (Newton in *Encycl. Brit.* xii. 139). To this family belongs the New Zealand "Tui" above mentioned; and it may be remarked that these birds as a rule feed on soft fruits, such as figs, and

bananas. It is to Acrulocercus, one of the Hawaiian genera of the Meliphagidæ, that Mr. Perkins refers me, on my asking him to name some of the fruit-eaters in that group.

These climbing shrubs, as Dr. Warburg observes, mostly frequent the tropical forests up to 4,000 feet and over. Though their most familiar habit is as tree-climbers in the forests, in localities where there are no trees they adopt a trailing habit and cover mountain peaks and ridges with a dense growth to the exclusion of almost all other plants. Many a peak in the Pacific islands would be inaccessible if it were not for the dense growth of these plants on their precipitous sides. It was owing to the friendly aid of a tangled mass of Freycinetia stems that Lieutenant Heming and myself were able to clamber to the summit of Fauro Island (1,900 feet) in the Solomon Group, where I discovered a tree that under the name of Sararanga forms the type of the third genus of the Pandanaceæ.

Whilst describing their station, it will be of interest to also record the altitudes at which these plants have been observed in the tropical Pacific. Since they can be independent of trees and are as much at home on treeless rocky peaks and mountain crests, the upper limit would usually be determined by climatic conditions, abundance of rain and great humidity being the chief requisites ; but, as will be seen below this limit, does not seem to be reached in the tropical islands of the South Pacific except perhaps in Tahiti. In the Fijis the Freycinetias ascend to the highest mountain peaks. Thus, three of the species discovered here by Seemann were found at elevations of about 4,000 feet on Voma Peak in Viti Levu and in the highlands of Taviuni. In Vanua Levu, as I found, they cover the highest peaks 3,500 feet above the sea. They are especially abundant on the lofty mountain ridges, and clothe the higher slopes of the Mbatini Ridge which terminates in the highest peak of the island. In no locality did I find them growing in such densely tangled masses as on the long ridge-like crest that forms the upper part of Mount Freeland, 2,740 feet above the sea. For more than an hour in order to reach the summit I had to clamber along the crest of a ridge covered with a dense growth several feet deep of these trailing plants, without touching the ground beneath.

In Samoa, as we learn from Reinecke, Freycinetias are common on the mountain ridges, climbing the trees and forming also a dense undergrowth covering the ground and concealing the rocks. They occur at all levels from 1,000 feet above the sea up to the highest region of Savaii, rather over 5,000 feet in elevation. In

Rarotonga, according to Mr. Cheeseman, the Freycinetias are very abundant on the mountains, which reach a height of 2,200 feet, the plants scrambling up the trunks of trees or over rocks and frequently rendering the forest almost impenetrable. In Tahiti, Nadeaud tells us, the Freycinetias often cover in an inextricable network the sides of the valleys at elevations of 2,000 to 3,300 feet, extending in their vertical range from the lower levels of the island to the highest inaccessible peaks which attain a maximum height of about 7,300 feet.

These plants in the Hawaiian group are common in the lower woods as Hillebrand informs us, that is to say, at elevations of 2,000 or 3,000 feet. During my descent from Mauna Kea through the Hamakua forests on the north-east side I observed that the Freycinetias commenced at an altitude of 3,900 feet, and that they attained their greatest development between 3,200 and 2,000 feet. These plants ascended quite a thousand feet higher on these mountain slopes than the Bird's Nest Fern (Asplenium Nidus), which reached an altitude of 2,800 feet. In the forests on the west side of Mauna Loa they were abundant at altitudes of 3,500 to 4,000 feet and were not noticed above 4,500 feet. On the slopes of Mount Eeka in West Maui they abounded between 3,500 and 4,400 feet. In those localities where the forest descends to the sea, Freycinetias occur at the coast, and on Oahu they are often found at elevations under a thousand feet.

I have but few data showing, the altitude obtained by Freycinetias in other regions, as, for instance, in their most southerly habitat in New Zealand, where they give a tropical luxuriance to the forests, or in their chief home in Malaya. From Schimper's observations (*Plant-Geography*, p. 293) it would seem that they thrive in the Gedeh forest of Java at elevations of about 5,000 feet. Except for the lower levels, Warburg makes but few references to this subject in dealing with the species. It appears to me that some very interesting results might be obtained by comparing the vertical range of this genus in different regions, as, for instance, in New Zealand and in Borneo or in Java. We might get indications that since the age of Freycinetia began the climate in tropical latitudes has been getting warmer, and that the erstwhile plants of the lower levels are now as a result climbing the mountain slopes. The student of distribution may find here a genus that has been "cornered" not only in space and time, but as regards its conditions of existence. Since it is obvious that during a gradual increase of temperature it would ascend the mountains and during a

lowering of temperature it would descend to the plains, it follows that in the mountains of an oceanic island it might be driven into the sea or await extinction on a mountain-top. In the tropics also there would be no escape during a gradual increase of temperature. Here again it would make its last stand on the strand, and, forced to choose between Death and Adaptation, the genus might select the latter alternative and present us with a startling new form. In this sense Freycinetia seems to offer itself as "fair game" for the speculative botanist, and at all events he will be able to interrogate it as to the connection between its existing range of altitude and the climatic conditions of the earlier phases of its history.

The Freycinetias bear the same name over Polynesia, "ie-ie" in Hawaii, "ie" and "ie-ie" in Tahiti and Samoa, which appear in their full form in the Rarotongan and Maori "kie-kie." The secret of the wide distribution of the name lies in the circumstance that this is a mat-word over much of Polynesia, as in Fiji, Tonga, Samoa, the Gilbert group, Tahiti, &c., Freycinetia leaves being often employed for making mats, as in Samoa and New Zealand. The same word is applied in some groups to small species of Pandanus that were also used in mat-making. Thus in Fiji "kie-kie" was not only the name for a mat-dress, but also of Pandanus caricosus that supplied the material. In the home of the Polynesians in Malaya and its vicinity the same word for mat and Pandanus occur. Thus, "gerekere" in the Motu dialect of New Guinea and "keker" or "kekel" in Amboyna are the names of small species of Pandanus employed in mat-manufacture; whilst "kihu" and "kiel" in Celebes are the words for the mats themselves. Therefore in one form or another the word, originally applied to the mats, but now often restricted to the plants from which the materials were derived, ranges over the great region extending from Malaya to New Zealand, Tahiti, and Hawaii, and, as I have shown in the table given in my paper on Polynesian Plant-Names (*Journ. Victor. Inst.*, London, 1896), it may be traced even to Further India, as in Annam, and to North-East Australia. It thus covers the area to which the migrations of the Polynesians of the Pacific have been confined, and it covers also the area of the genus Freycinetia. There is something far more than mere analogy between man and plants in their occupation of the Pacific islands. The plants are Malayan and the Polynesians are from Malaya also, whilst in both man and plants we experience the same difficulty in explaining their dispersal over the ocean. Divesting his mind of all previous conceptions, the ethnologist might profitably study

de novo the dispersion of man in the Pacific from the standpoint of plant-dispersal (see Chapter XXVIII).

SAPINDUS AND PHYLLANTHUS.

Brief reference can alone be made to these two genera. Foremost comes Sapindus, which is represented by two endemic species, one in Hawaii and one in Fiji, and by another species, found in Tahiti, the Marquesas, and Easter Island, which is identified by some botanists with the well-known American "soap-tree," S. saponaria. There are several difficulties connected with the presence of this genus of the Old and New World in the Pacific. Not the least of them is connected with the transport of the large seeds of this genus, an inch in size, to the isolated Hawaiian Group, where it is represented by a solitary endemic species in the island of Oahu. The fleshy mesocarp of the fruits might attract birds; but it is not easy to perceive how birds could carry such large seeds over some 1,500 or 2,000 miles of ocean. Yet the same difficulty exists with a few other genera, such as Osmanthus and Sideroxylon, that are only represented in Hawaii by endemic species, genera which require the agency of birds to explain their occurrence unless we wish to postulate a continental connection for this group. (See under those genera in Chapter XXVII.)

The large Euphorbiaceous genus Phyllanthus, spread universally over the tropics and containing some 500 known species, clearly indicates by its distribution in the Pacific islands that genera with dry fruits, such as are typical of the order, are as widely distributed and just as much at home in these islands as the genera with fleshy fruits, such as Psychotria and Cyrtandra. The small trees and shrubs of Phyllanthus are common in dry, open, partially wooded districts near the sea-border. The genus attains its greatest development in this ocean in New Caledonia and Fiji; and since the number of species diminishes the further we penetrate the Pacific, it can be scarcely doubted that the genus has entered this ocean from the west. In Fiji there are at least 20 species, of which probably half are not recorded from elsewhere. In Samoa there are seemingly but few peculiar species. In Hawaii there is only one indigenous species, and that is endemic. The genus, however, has developed a lesser centre of distribution in East Polynesia, there being about a dozen species known from Tahiti and the Marquesas, of which half are peculiar to one or other of those groups. From experiments made by me in Fiji

on the fruits and seeds of two species it was evident that they possessed little or no capacity for dispersal by the currents. We look, therefore, to the birds, and in this connection it is of interest to note that this genus is included amongst those known to be dispersed by birds in the Pacific, some of the fruits having been found in the crops of fruit-pigeons shot by Prof. Moseley in the Admiralty Islands (*Bot. Chall. Exped.*, Introd. 46 ; iv. 308).

PRITCHARDIA (Palmaceæ).

This genus of Fan Palms supplies an instructive lesson for the student of plant-distribution, more especially with reference to the loss of the endemic reputation of a genus. Regarded by the earlier botanists who visited the Pacific as identical with the familiar Asiatic Talipot Palm (Corypha umbraculifera), the Fan Palms of this region, as represented in Fiji and Hawaii, were subsequently placed by Seemann and Wendland in a new genus restricted to Polynesia and named after a former British Consul in Fiji. Since that time it has lost its reputation as a peculiarly Pacific genus, since a species (Pritchardia filifera) has been found lingering in a few valleys in Arizona, where it enjoys the distinction of being the most northerly in station of all the world's palms (Linden in *Illustr. Hort.* vol. 24, 1876–77). It would thus appear that the Pacific islands have derived this genus of palms from the western part of North America, but the whole question is beset with many difficulties, and not the least is that connected with the confusion that seems to reign in several cases as regards the allocation and identity of the species.

Six species are named in the *Index Kewensis*, viz.: Pritchardia macrocarpa, restricted to Hawaii ; P. martii and P. gaudichaudii, of the Pacific islands ; P. pacifica, assigned to Fiji ; P. vuylstekeana, from the Paumotus ; and P. filifera, from the west side of North America. Though it is sometimes difficult to reconcile this account of the distribution of the genus in the Pacific with views held by other botanists, it offers the safest basis for the future investigation of the subject. It would be, however, necessary to remember that Pritchardia gaudichaudii and P. martii are regarded by Hillebrand as peculiar to the Hawaiian Islands, and that the exact locality of the Paumotu species is not very definitely settled, if it depends on the remarks made on this species in the *Gardeners' Chronicle* for 1883. No mention is indeed made by Drake del Castillo of any Tahitian or Paumotuan species.

Whilst in Hawaii and Fiji I was much interested in these palms, and the following remarks are merely intended to be a contribution to the subject. According to Seemann, Hemsley, Drake del Castillo, and Burkill, Pritchardia pacifica, which often attains a height of thirty to thirty-five feet, occurs in Fiji, Tonga, Samoa, and the Marquesas, but it does not exist in Tahiti, and Cheeseman does not include it in the Rarotongan flora. Except in the Tonga Group, where, according to Lister as quoted by Hemsley, the palms form conspicuous objects along the weather shore of the island of Eua, this species is rarely found in the wild state in the South Pacific. This especially applies to Fiji, as Mr. Horne also observes ; and at most one is accustomed to see (to employ the words of Dr. Seemann) one or two trees outside a village which are reserved, as in many parts of Polynesia, for the use of the chiefs who employ the leaves for fans and for other purposes. But even this reason for preserving the palms scarcely now exists in Fiji, and at the time of my sojourn in Vanua Levu (1897–99) the trees were rare enough to be regarded as curiosities. In the Marquesas, according to Bennett (quoted by Seemann), they grow in groves in the valleys of the interior. Dr. Reinecke does not even include the species in the Samoan flora, but mentions it with the Date-Palm (Phœnix dactylifera) as if it were recently introduced. It was, however, found in that group by the United States Exploring Expedition about 1840, and this is evidently the palm referred to by Captain Cook as existing at his time in the Tongan Group.

The Hawaiian species of the palm appear to be three in number, Pritchardia gaudichaudii and P. martii, both regarded by Hillebrand as confined to the group, and P. macrocarpa of Linden, also endemic (*Illustr. Hort.* vol. 26). The two first-named species are evidently on the road to extinction in the wild state, and often find their last refuge on rocky, almost inaccessible, inland cliffs. Pritchardia gaudichaudii, about twenty feet in height, is found in the wild state, as we learn from Hillebrand, on the islands of Molokai and Hawaii. It was at one time frequently met with near native dwellings ; but during my sojourn in 1896–97 on the last-named island it was not at all frequent, and as a rule only came under my notice occasionally in clumps of three or four trees on the Kona and Puna coasts, as near Kiholo, Milolii, and Kalapana. However, it was more frequent in the Waimanu district of Kohala in the same island. Here I noticed it growing in clumps in precipitous rocky situations at elevations ranging

from 1,200 to 2,000 feet. The other palm mentioned by Hillebrand, P. martii, is only five or six feet high, and is confined mostly to Oahu and Molokai.

The agency of man in introducing these interesting Fan-Palms into the Hawaiian Islands seems out of the question, since they are home productions in a specific sense and are doubtless ancient components of the flora ; and, of course, grave objections exist on ethnological grounds, if this genus had originally its home in America. With reference, however, to Pritchardia pacifica of the South Pacific, it is not unlikely that man has aided in the distribution of a palm mainly preserved by planting in and about the villages and set apart from time immemorial for the use of the chiefs.

In this connection the aboriginal names are of some importance and may be very briefly here referred to. The Fijian "Viu," the "Piu" of Samoa, Tonga, and Futuna, and the Tongan "Biu" are forms of the same name applied to this palm all over West Polynesia ; and I have shown in my paper on Polynesian Plant-Names that in the form of "Firo" in the Solomon Islands (Bougainville Straits) and of "Wiru" in Sundanese, one of the Malayan languages, the same name is given to another genus of Fan Palms, namely, Licuala. But since these West Polynesian names do not always conform with the laws of consonantal interchange in this region, they cannot all be considered as indigenous in the languages concerned. If, for instance, "Viu" is an indigenous Fijian name, as no doubt it is, since it follows the phonetic laws affecting the Malayan and Fijian languages, "Piu" must be a foreign word in Samoa and Tonga, and "Biu" must be another introduced Tongan name. . . . The Fijians have in "Sakiki" (contracted into "Saii" in the Somosomo dialect) another name for this palm. This is probably derived from "Kiekie," a mat-word in different forms in various Polynesian groups, and applied in many islands to the plants that supply the materials for mat-making, such as Pandanus and Freycinetia.

The Hawaiian generic name of "Loulu" for these palms appears to be quite local ; but it may possibly have a common origin with "Roro," one of the Fijian names of Cycas circinalis. It is pointed out by Hillebrand that the Hawaiian name of the edible kernels of these palms, "Hawane" or "Wahane," occurs in the Marquesas as "Vahana" applied to the palm, a comparison that is on linguistic grounds quite legitimate. "Vaake" is another Marquesan name, which recalls "Vakoa," the Malagasy word for Pandanus.

When we compare the variety of the names of the Pritchardia fan-palms in the Pacific Islands with the prevailing uniformity of the names of cultivated plants transported by the aborigines in their migrations from Malaya, such as the taro, the yam, the sugar-cane, the coco-nut, and the Malay-apple, we perceive that the testimony of the names points to the same conclusion as the botanical evidence, namely, that the ancestors of the Hawaiians found these palms in the group at the time of its occupation. In the South Pacific much uncertainty prevails. The ancestors of the West Polynesian peoples evidently brought the word for a fan-palm from their Malayan home; but it is doubtful if they found Pritchardia already established in all the islands; and the apparent home of the genus in America prevents us from attributing to a palm, that is by some botanists regarded as confined to the Western Pacific, a home in the neighbouring regions to the west. There is thus a lack of agreement between the botanical and ethnological indications as regards the original American origin of Pritchardia in the South Pacific.

There remain then the agencies of the currents and of birds. A singular feature in the distribution of the Hawaiian species, Pritchardia gaudichaudii, at once affords a clue as concerning the dispersal in the North Pacific. Dr. Hillebrand remarks that this palm covers part of Bird Island, a small volcanic rock forming an outlier of the Hawaiian group about 400 miles north-east of Kauai. Here the agency of birds is suggested, since it is scarcely likely, though, as shown below, not impossible, that stranded fruits of the palm could have established themselves in this fashion. Mr. Perkins has an interesting note on the food of Ciridops anna, an Hawaiian bird, now nearly extinct, that feeds principally on the blossoms and unripe fruits of the Loulu palms, probably of this species. The drupes when fresh have a somewhat fleshy mesocarp and are about $\frac{9}{10}$ of an inch (22 mm.) across, and their crustaceous inner shell would undoubtedly fit the seeds for dispersal by frugivorous birds like pigeons. The fruits of the other two Hawaiian species are considerably larger, that of P. macrocarpa being, according to Linden, of the size of a nut of Juglans regia, that is, about $1\frac{1}{8}$ inch or 29 mm., whilst that of P. martii, as we learn from Hillebrand, is from $1\frac{1}{2}$ to 2 inches or 37 to 50 mm. Allowing for the variation in size of the fruits within the limits of the genus, there need be no more difficulty in assuming that the original species had fruits that could have been brought by birds, than in holding that the fruits of Elæocarpus have been carried to Hawaii in the

same fashion. The drupes of Pritchardia pacifica are barely half an inch in diameter. They are fitted by reason of their hard crustaceous endocarp for dispersal by fruit-pigeons; and I may here add that these birds are known to distribute the fruits of other palms, such as Kentia and Areca, in the islands of the South Pacific (*Bot. Chall. Exped.* iv. 308, 312).

Both in Hawaii and in Fiji I experimented on the capacity of Pritchardia drupes for dispersal by the currents. Those of the Hawaiian species, P. gaudichaudii, have when well dried a light buoyant rather fibrous mesocarp which enables them to float in the case of a good proportion of the fruits for at least five weeks. I had no opportunity of testing the buoyancy of the fruits of P. martii, another Hawaiian species; but, judging from the existence in the coats of a fibrous layer as described by Hillebrand, they ought to display some floating power. The fruits of P. pacifica, the South Pacific species, lack the light buoyant covering of the Hawaiian species above referred to, and display little or no floating power even after drying for weeks. Looking at the results of these experiments, it would seem that it is not impossible that Hawaii received the genus through the agency of the currents; but it seems scarcely probable, since it could only have been derived from America, and the American species grows in the interior of the continent and not near the sea-border. The possibility of course exists; but I am inclined to attribute the presence of Pritchardia in Hawaii to bird-agency.

My position from the standpoint of dispersal with regard to Pritchardia in the Pacific is this. The Hawaiian species I would consider as American in origin. The Marquesan species, unless recently described, still awaits detailed investigation. The West Polynesian species of Fiji and Tonga, according to the principles of distribution prevailing in the South Pacific, ought to hail from the west.

Summary.

(1) Whilst the earliest age characterised by the Coniferæ was restricted to the Western Pacific, and whilst the following age of the Compositæ and Lobeliaceæ, mainly American in their affinities, was concerned with the regions of Hawaii and Tahiti, we have now to discuss the Malayan era during which the bulk of the plants were derived from the nearest tropical regions of the Old World. Here we have to deal with the low-level flora of Hawaii, that is to say, with the plants of the levels below 4,000 or 5,000 feet, and with

almost the entire floras of the areas of Fiji-Samoa and of East Polynesia. The whole of the tropical Pacific is here concerned, and not a portion of it, as in the two preceding eras; and in our comparison we shall see that there are two, and not as heretofore three, regions to be regarded—the Hawaiian in the North Pacific, and the whole Polynesian area of the South Pacific extending from Fiji to Tahiti.

(2) Here the frugivorous bird has been the principal agent in dispersing the plants, quite two-thirds of the genera possessing drupes or berries that would attract such birds.

(3) The genera representative of the first part of this era are those which have only peculiar species in Hawaii, and are composed in the South Pacific either entirely of peculiar species or sometimes of a mixture of endemic and non-endemic species. It is an era of complete isolation in Hawaii and often of a partial connection between the groups of the southern region. Except to some extent in the South Pacific, the dispersing agencies are now no longer active between the groups.

(4) Amongst the genera typical of this period are Pittosporum, Gardenia, Psychotria, Cyrtandra, and Freycinetia.

(5) The two genera of the Rubiaceæ, Psychotria and Coprosma (the last belonging to the mountain-flora), appear to be well suited for the investigation of the effect on distribution of the geographical position of the home of the genus, the first with 600 to 700 species distributed over the tropics of the Old and New Worlds, the second with some sixty species having its home in New Zealand.

(6) From the Pacific Cyrtandras we derive the lessons that the display of great formative power in a genus may not be a peculiarity of an insular flora; that the isolation of an oceanic archipelago does not necessarily induce "endemism," but merely intensifies it; and that the production of new species within the limits of a genus like Cyrtandra may be nearly as active on the mainland as in an island in mid-ocean.

(7) From the Freycinetias we learn that it may be possible to connect the distribution of a genus of plants with that of a genus or a family of birds. Just as in Chapter XXIV we endeavoured to connect Coprosma and Porphyrio (the Purple Water-Hens), so we here suggest a connection, in their range over the Pacific, between the Freycinetias and the Meliphagidæ (the Honey-eaters), a connection that in the last case at least belongs to the past.

(8) From the genus Phyllanthus we learn that genera with dry fruits may be as widely distributed and may display the same

formative power in the Pacific as those with fleshy fruits that would seem much more likely to be dispersed by birds. Here again we obtain an indirect indication that species-making in these islands is not altogether dependent on isolation.

(9) In the case of the genus Sapindus we are apparently compelled to infer that its large seeds (in the present species an inch in size) have been transported by birds to Hawaii. Yet in point of size the difficulties here raised are no greater than those arising from the existence of such genera as Sideroxylon and Elæocarpus in Hawaii, the fruits of which are known to attract frugivorous birds.

CHAPTER XXVI

THE MALAYAN ERA OF THE NON-ENDEMIC GENERA OF FLOWERING PLANTS (*continued*)

THE AGE OF WIDE DISPERSAL OVER THE TROPICAL PACIFIC (*continued*)

The widely dispersed genera that are as a rule not entirely represented by endemic species in any archipelago.—Elæocarpus.—Dodonæa.—Metrosideros. — Alyxia. — Alphitonia.— Pisonia.— Wikstrœmia.— Peperomia.—Eugenia.—Gossypium.—The last stage in the general dispersal of plants of the Malayan era as illustrated by the widely-dispersed genera having as a rule no peculiar species.—Rhus.—Osteomeles.—Plectronia.—Boerhaavia.—Polygonum.—Pipturus.—Dianella.—Summary.

A LATER period in the era of the general dispersal of Malayan plants over the Pacific is indicated by those genera that as a rule are never entirely represented by endemic species in any archipelago. Hawaii now comes into touch with the world outside, and all the groups possess some connecting link. But the beginning of the effect of the isolating influence is shown in the association in each principal archipelago of peculiar species with those that occur in other groups.

We see here illustrated in all but the final stage that process by which a solitary widely-ranging species, alone representing its genus, becomes ultimately in each group the parent of a number of peculiar species. The polymorphous, or extremely variable, species plays in this period the all-important part. The earliest stage is exhibited by such genera as Alphitonia, Dodonæa, Metrosideros, Pisonia, and Wikstrœmia, that possess in the tropical Pacific a solitary widely-ranging species, varying independently in every group and giving rise to forms that, in their degree of differentiation, sometimes approach a specific value. Later stages are shown

when the polymorphous species, having done its work of distributing the genus, settles down and "differentiates" in every group; and this we see now illustrated in the genera Elæocarpus, Alyxia, Peperomia, and others.

The bulk of the genera of this period, of which only a few can be mentioned here, hail from the tropics of the Old World through Malaya. Thus Alyxia, Elæocarpus, Morinda, and Wikstrœmia are Malayan; whilst genera like Eugenia, Peperomia, and Pisonia, that occur in the Old and New Worlds, can similarly be traced to the Asiatic side of the ocean by the distribution of their species. Others again have their home in New Zealand like Metrosideros, or in Australia, as with Dodonæa and Scævola. None are exclusively American. Some of the genera, as Morinda and Scævola, have littoral as well as inland species; but, as shown in Chapter XIV, there is rarely anything to suggest a derivation of the inland from the coast species, both being, from the standpoint of dispersal, of independent origin.

About half of the plants have fleshy or sappy fruits (drupes and berries) that would attract frugivorous birds, such as we find in Xylosma, Elæocarpus, Eugenia, Scævola, Wikstrœmia, &c., whilst the others have often dry capsular fruits, with minute seeds as in Metrosideros, or with larger seeds as in Dodonæa. Some of them, like Pisonia, have fruits that excrete a viscid material that causes them to adhere firmly to plumage. Birds both granivorous and frugivorous have been actively at work; and there are few difficulties relating to dispersal connected with the genera, except with such as Gossypium and Elæocarpus.

I will adopt the method employed in the preceding chapter of discussing in detail from the standpoint of dispersal some of the genera that came most frequently under my notice, or in which I am greatly interested, and of dealing briefly with some of the rest. Those dealt with in other connections will not be treated.

ELÆOCARPUS (Tiliaceæ).

This is a genus of trees containing, according to the *Index Kewensis*, about 130 species, most of which are confined to tropical Asia, including Malaya; but a fair number occur in the Pacific region, in Australia, New Zealand, and the islands of the tropical Pacific, and the genus is also found in Japan. It will thus be seen that Elæocarpus is not only a continental but also a typical insular genus. It has reached not only some of the most isolated island-

groups of the Pacific, but it is to be found also in the smaller islands of the Indian Ocean, there being an endemic species in Mauritius. Amongst the Pacific Islands, a region with which we are more immediately concerned, it has been recorded from the Solomon Islands, New Caledonia, Fiji, Tonga, Samoa, Rarotonga, and Hawaii. It is strange that the genus is not accredited to Tahiti, but since it is represented in Rarotonga we may regard it as not altogether absent from East Polynesia. Reinecke does not include it amongst the Samoan plants, but Horne, in a short list of plants collected in Upolu about 1878, mentions Elæocarpus græffei, a Fijian species (*Year in Fiji*, p. 285).

New Caledonia represents the principal centre of the genus in the tropical Pacific, thirteen species being accredited to it in the *Index Kewensis*. Seemann found six species in Fiji, a number that does not seem to have been added to by Horne. Of these one is found in Tonga and Samoa, and of the rest perhaps most are peculiar; but one of them is closely allied to a second peculiar Tongan species. Tonga possesses the two species just alluded to, whilst Rarotonga and Hawaii have each a peculiar species.

From an interesting comparison made by Mr. Burkill of some of the Polynesian species, it would seem that Elæocarpus, if not actually possessing a widely-spread polymorphous species in the tropical Pacific, presents us with the next stage in the differentiation of the species. Thus, he says in his paper on the flora of Vavau that an endemic Tongan species, E. tonganus, is allied to three different species—E. græffei from Fiji, E. floridanus from the Solomon Group, and E. glandulifer from Ceylon—three species, he remarks, which are "so closely allied that it is possible to regard them as insular subspecies." It would thus appear that some of the species of the Western Pacific are almost in touch with Asiatic species. It would be of importance to determine whether some affinity can be detected between the species of this part of the Pacific and some of the widely-ranging species of Indo-Malaya, such as E. ganitrus and E. oblongus. Mr. Burkill goes on to say that the solitary Hawaiian and Rarotongan species are closely allied, an inference which is of interest as indicating the route by which Hawaii received its species. The genus, we may fairly infer, once possessed a widely-ranging polymorphous or very variable Asiatic species in the tropical Pacific; and we see it now in the next stage of specific differentiation in various far-removed regions. In this connection Seemann significantly remarks that all the Fijian species are evidently very local in the group.

It will be appropriate here to refer briefly to the station and mode of occurrence of the species. They occur most typically as forest-trees, often of considerable height. In New Zealand, according to Hochstetter, they form a feature in the temperate rain-forest; and, as we learn from Kurz, they are similarly conspicuous in the tropical rain-forests of Pegu. To this seeming indifference to the varying thermal conditions of different latitudes we shall have subsequently to refer again. The tree of the Hawaiian Group, as Hillebrand tells us, is common in the forests of Oahu and Kauai, but is scarce in Maui and Hawaii, a singular distribution that may be due to the inflorescence being "often monstrously deformed by oviposition of some dipterous insect." The Rarotongan species, according to Cheeseman, is common throughout the island from the sea-level to the tops of the hills. In Vanua Levu I found that these trees preferred the crests of wooded mountain-ridges or the partially vegetated mountain peaks. They came under my notice in the forests of the island of Fauro, in the Solomon Group, associated with other large trees of the genera Canarium and Calophyllum.

Much interest is attached to the mode of dispersal of this genus, since in some species the size of the drupes and of the included "stone" is so great that, judged by those species only, it might be deemed impossible to attribute the existence of the genus in isolated oceanic groups to the agency of frugivorous birds. We are, however, compelled to appeal to the bird, since, as my experiments in Fiji indicate, the genus has little or no capacity for dispersal by currents, the "stone" when containing a seed always sinking, whilst the entire fruit either sinks at once or floats heavily for a few days.

The degree of fleshiness of the drupes of Elæocarpus varies in different species, being sometimes slight and at other times pronounced, but, speaking generally, they would be expected to attract frugivorous birds. The colour of the fruits of some species is dark and purplish, whilst in others it is a bright blue. In the last case the fruits are very conspicuous and sappy. A Solomon Island species collected by me and a Malayan species observed by Ridley had bright blue fruits, and Cheeseman refers to the Rarotongan species as possessing fruits of this hue. Their colour, therefore, would often aid in attracting birds, and we are not surprised to learn that they form a favourite food with fruit-pigeons, parrots, and other frugivorous birds in different regions. Amongst the fruits found by Professor Moseley in the crops of fruit-pigeons

in the Admiralty Islands were those of Elæocarpus; whilst in the Solomon Islands I noticed that the blue fruits of the "Toa," a species of the genus, were a favourite food of the same birds (*Bot. Chall. Exped.*, iv. 307, 308; Guppy's *Solomon Islands*, 293, 295). We learn also from Hochstetter and from Sir W. Buller that the drupes of the "Hinau" (Elæocarpus) form a favourite food of the parrots and fruit-pigeons of New Zealand (Hochstetter's *New Zealand;* Buller's *Birds of New Zealand*).

The question of size acquires considerable importance when we come to consider the transport of the seeds of the genus to a group of islands lying, like Hawaii, in the middle of the Pacific Ocean. The protection of the seed is also another important matter. There can, however, be no doubt that the hard woody or often osseous "stone" sufficiently protects the seed. With regard to size, if we were to judge from the dimensions of the fruits of some of the Fijian species, where, as I found, the "stone" measures from 3 to 5 centimetres ($1\frac{1}{4}$ to 2 inches) in length, we might be led to form a very erroneous opinion of the capacity of the genus for conveyance through the agency of frugivorous birds to Hawaii. But when we turn to the Hawaiian species we find the difficulty much diminished, though still serious, the fruits being smaller and possessing a "stone" $2\frac{1}{2}$ centimetres or about an inch long. In other regions, however, the genus may possess fruits yet smaller in size. The Tongan endemic species, as described by Burkill, has fruits 1·7 cm. or $\frac{7}{10}$ of an inch in length; and closely similar dimensions are given by Kirk for a New Zealand species. In both these cases the "stone" would not be more than half an inch or 1·2 cm. in length, and this would also apply to the Solomon Island species above mentioned. In another New Zealand species, where the drupe is only half an inch, the "stone" would be still smaller. It is thus evident that the fruits of different species vary greatly in size in different regions, and that there is no difficulty in assuming that a small-fruited species could be dispersed over the Pacific by frugivorous birds, and carried either to Hawaii or New Zealand.

It might be an interesting point to determine to what extent a species in an oceanic island could effect its own isolation by developing a "stone" too large and too heavy to be transported across an ocean by birds, such as seems to have happened with some Fijian species. But a similar curious question is raised by the deterioration of a drupe in its capacity for dispersal by frugivorous birds, when, as in the case of the Hawaiian species

of Elæocarpus, the drupes become dry and almost sapless. As remarked in Note 68, this same feature is to be noticed in the fruits of some of the Hawaiian endemic genera. This, of course, would be quite in accord with what we should expect from the standpoint of dispersal.

I will conclude these remarks on Elæocarpus with a reference to the similarity of its distribution with that of Freycinetia. Both genera are at home in the temperate rain-forests of New Zealand and in the tropical rain-forests of the Pacific islands and of Malaya. Their capacities for dispersal are so different and so unequal, the dispersal of Freycinetia being seemingly so much more readily effected, that we can only suppose that time has long since discounted any special advantage one genus possesses over the other as regards distribution.

DODONÆA (Sapindaceæ).

This genus of small trees and shrubs includes between fifty and sixty known species, of which about forty are confined to Australia; but a few species are found over the tropical and subtropical regions of the world, extending sometimes into temperate latitudes. There are, it seems, only three species known from the oceanic groups of the tropical Pacific: one, the cosmopolitan Dodonæa viscosa, that occurs in every island of volcanic formation; and two others associated with it in the Hawaiian Group, to which they are restricted. We have thus repeated in this genus what is true of several other genera in Hawaii, such as Metrosideros and Wikstrœmia, namely, the occurrence in that group of a widely-ranging species accompanied by other species peculiar to those islands. In the case of Dodonæa in Hawaii we should not expect to find it very difficult to connect the endemic species with the widely-ranging D. viscosa, which is a very variable species. The extreme forms in different parts of the world are so different in character that Bentham viewed this species as probably including the whole of the extra-Australian species, excepting perhaps the Hawaiian endemic species and one or two South African and Mexican plants (*Bot. Chall. Exped.*, iii. 136).

Of the two Hawaiian peculiar species, one, Dodonæa eriocarpa, is a mountain shrub found in most of the large islands and occurring sometimes at elevations of 6,000 to 8,000 feet. The other species, D. stenoptera, is, according to Hillebrand, a very distinct species found only on Molokai. Bentham was only acquainted

with the first-named, and his hesitation to include it as one of the innumerable forms of the widely-ranging D. viscosa is very suggestive. However, whether or not one or both of these peculiar forms are connected in their origin with this species, it is certain that the genus has been established for ages in Hawaii ; and from D. viscosa we can learn how a species of the genus can cross an ocean, and also how from a widely-ranging species exhibiting extreme variability species peculiar to a group of islands could have been derived.

The great variability of Dodonæa viscosa is associated with great adaptability to different stations. Thus, as Mr. Hemsley tersely puts it, it is one of those plants that thrive on the sea-coast as well as inland, and in almost any soil or situation—provided, it may be added, that the station is well exposed to the sun. Although Mr. Ridley characterises it as a regular sea-shore plant in the Malay peninsula, and although Prof. Schimper places it in the Indo-Malayan strand-flora, it is as an inland plant that it is most characteristic of the Pacific islands ; and the key to its powers of adaptation to different stations is to be found in its xerophilous habit. It is essentially a plant of sunny places, and is equally at home on the parched inland plain, in the open wood, on the sandy beach, on an old lava-field, or on rocky declivities. It is not a plant of the rain-forest, preferring dryness to humidity and sunshine to shade.

The following remarks on the mode of dispersal of the wide-ranging Dodonæa viscosa will serve to roughly indicate the capacity of the genus for distribution. It is a subject, however, that requires further detailed investigation. The light, inflated, winged capsules of this species, about an inch across, could be blown for long distances along the ground and carried for short distances in the air by strong winds, but, as is also remarked by Prof. Schimper (*Ind. Mal. Strand-flora*, p. 157), they are much too large to be transported by winds across a broad tract of sea. The currents, however, may have aided in the dispersal of the species in the case of island-groups 500 or 600 miles apart. Although the membranous capsules before dehiscing would be unable to withstand the " rough-and-tumble " of ocean-transport for more than a few days, the seeds possess some floating powers of a purely accidental nature due to the imperfect filling up of the seed-cavity in some of the seeds. In an experiment made in Hawaii I found that only half the seeds floated in sea-water. Prof. Schimper, in an experiment conducted in Germany with seeds that must have been

well dried by keeping, found that they floated for from ten to sixty days. This limited capacity for flotation might possibly allow the species to reach Tahiti by easy stages from Fiji; but it is not sufficient to explain its occurrence in the more isolated Hawaiian Group. The fruits and seeds of this plant never, however, came under my notice in the floating or stranded seed-drift of Fiji; and I am not inclined, for this and the reasons above mentioned, to consider that the currents have been very effective agents in dispersing this plant over the Pacific islands.

Hillebrand endeavoured to account for the wide distribution ot Dodonæa viscosa by "the glutinous capsules which would easily adhere to the plumage of birds." It may be here remarked that in the dried state specimens of the plant have a varnished appearance as respecting the leaves, branchlets, and capsules. In the living condition this is represented by a glutinous or viscid condition of the surface of these portions of the plant, rendering them adhesive to the touch. I found, however, that only the immature capsules are markedly "sticky," and that in any case the adhesive power was quite insufficient to allow of adherence for any length of time of fruits of this size to a bird's feathers. Mr. Ridley, who allows much latitude to birds in matters of dispersal, remarks that the stickiness only appears when the specimen is dry (*Trans. Linn. Soc. Bot.*, 1888–94, p. 289). It is, nevertheless, likely that the crustaceous seeds, which do not exceed $\frac{1}{5}$ of an inch (5 mm.) in size, when swallowed by a bird granivorous in its diet, might be voided unharmed, and the dispersal of the species assured. It is in this fashion, I imagine, that the plant reached distant groups like Tahiti and Hawaii.

There is, of course, the possibility that man has in past times aided in the distribution of Dodonæa viscosa over the warmer regions of the globe. But such an agency seems largely discounted in the case of an isolated archipelago like Hawaii by the occurrence of endemic species. Nor does the usual station in the Pacific islands support the view that it was introduced by the aborigines. According to Hillebrand, it possesses a variety (var. spathulata) in Hawaii which seems also to occur in Tahiti and New Zealand. Nadeaud observes that in Tahiti it grows as a bush on dry crests, and as a small tree, ten feet in height, in the mountains.

Nor do the aboriginal names of Dodonæa viscosa point in the direction of man's agency. It possesses a different name in every group, and is evidently not a plant with which the ancestors of the Polynesians were familiar in the home of the race. Thus it is

named "aalii" in Hawaii, "apiri" in Tahiti, "ake" in Rarotonga, "lala vao" in Samoa, and I may add "usi" or, as Seemann writes it, "wase" in Fiji.

Looking at these various facts, I am not inclined to exclude altogether any one of the three agencies above discussed; but I should imagine that, placed in their order of effectiveness, we should have first birds, then the currents, and lastly man.

METROSIDEROS (Myrtaceæ)

Whilst this genus of trees and shrubs has its home in New Zealand and Australia, there is an extremely variable Polynesian species, Metrosideros polymorpha, ranging over all the volcanic groups of the tropical Pacific, from Fiji to Pitcairn Island and from Hawaii to the Kermadec group, but seemingly only in the Hawaiian group associated with endemic species. According to the *Index Kewensis* the genus comprises about forty known species, of which two-thirds are confined to New Zealand and Australia in equal proportions; whilst, among the rest, six species belong to New Caledonia, two to Hawaii, and three to Malaya, and there are solitary species in Chile, Madagascar, and South Africa.

I will attack the problem connected with the distribution of the genus through the widely-ranging Polynesian species, Metrosideros polymorpha. "This genus," wrote Dr. Seemann, "is in a fair way of becoming in Polynesia what Rubus is in Europe. It is very much given to variation, and it is very difficult to find out the limits of the different species." In making these remarks he had this species in view, and his adoption of Gaudichaud's specific name of "polymorpha" to cover almost all the Polynesian forms has been generally followed. Although so widely distributed over the Pacific, it is in the Hawaiian Islands that this tree attains its greatest development, growing gregariously and often forming almost exclusively entire forests; and it is here that it displays the greatest variation. But it was remarked by Seemann, and this was confirmed by Hillebrand, that almost all the Hawaiian forms occur in the Society or Tahitian Islands.

In connection with the great variability of Metrosideros polymorpha must be considered its variety of stations and its great range in altitude. Hillebrand describes seven Hawaiian forms of this species, and their various stations and characters are well illustrated in his descriptions. Thus, whilst the trees may attain a height of forty feet in the forests, in elevated exposed situations

they may be small and gnarled or low and shrubby; whilst in the bogs and swamps of the high levels of Maui and Kauai the plant grows as a prostrate shrub. It is not at all unlikely that the two peculiar Hawaiian species of the genus had a common origin from a widely-ranging species, which, if not the present M. polymorpha, was its immediate ancestor. One of them was, indeed, included by Dr. Seemann within the wide limits of this species, and the other was accepted with a doubt.

To illustrate the great vertical range in the Hawaiian Group of Metrosideros polymorpha, I will take it as I found it in the island of Hawaii. Here it ranges from the coast up to about 8,000 feet above the sea. But it is in the middle forest-zone at elevations of 2,000 to 4,000 feet, where it is often associated with the Koa and Olapa Trees (Acacia koa and Cheirodendron Gaudichaudii), that it is most at home and attains its greatest size. Higher up at heights of 5,000 to 7,000 feet in the more open forests it is still in the company of the trees just named together with Sophora chrysophylla and Myoporum sandwicense. At 8,000 feet it becomes very stunted and is accompanied usually by bushes of Cyathodes and other plants of similar bushy growth. In the lower parts of its range, from 2,000 down to 1,000 feet, it forms forests with the Kukui Tree (Aleurites moluccana), mingled also with smaller trees such as the Hawaiian Olive (Osmanthus), and the Kopiko (Straussia). Below 1,000 feet, and wherever bold promontories reach the coast and the inland forest descends to the sea, we find it associated with such trees and shrubs as the Lama (Maba sandwicensis) and different Akeas (Wikstrœmia). On the partially vegetated surfaces of old lava-flows near the coast it grows beside bushes of the Ulei (Osteomeles anthyllidifolia) and of Cyathodes.

Compared with its behaviour in Hawaii, Metrosideros polymorpha takes a relatively unimportant part in the vegetation of Fiji. As Horne observes, the trees are most common in the dry parts of the two largest islands and grow in the poorest soil. I found them in Vanua Levu usually in open exposed situations, generally in the dry "talasinga" plains on the north side of the island, where they were associated with Acacia Richii, Dodonæa viscosa, and Casuarinas; and sometimes they occurred in a shrubby form on the rocky peaks of the highest mountains. In Rarotonga also, as we learn from Cheeseman, it is on the tops of the rocky peaks and along the crests of the ridges that this species, which is abundant in the island, is frequently found.

I may here allude to the curious fact observed by me on the

upper open wooded slopes of Mauna Kea at elevations of 6,000 to 7,000 feet, and therefore on the outskirts of the true forest-zone. Here the Ohia Tree, as the Hawaiians name Metrosideros polymorpha, often grows in close association with the Olapa Tree (Cheirodendron Gaudichaudii). In one locality, for instance, a large Olapa was growing in the fork of an Ohia at about eight feet from the ground, and sending down roots on either side. Sometimes the trunks of the Olapa and the Ohia were to be seen growing in such close contact as to look like one tree. In one such case a young tree, four feet high, of Myoporum sandwicense was growing in a fork of the Ohia, whilst in a fork of the Olapa a plant of Vaccinium penduliflorum, three or four feet in height, had established itself. This remarkable instance of epiphytic growth also proved to be quite a revelation with regard to the dispersal of seeds in this island. Amongst these four associated plants, which include three trees and one shrub, all except the Ohia, which was probably the original tree, have fruits that would attract frugivorous birds ; and in succession these birds had first dropped a pyrene of the Olapa in the fork of the Ohia, and afterwards the seeds of Myoporum again on the Ohia, whilst finally the Vaccinium seeds were dropped into the fork of the Olapa after it had developed into a tree.

The mode of dispersal of the seeds of Metrosideros polymorpha now invites our attention. Since the fruits are dry, dehiscent capsules possessing minute fusiform seeds, we are not able to appeal directly to the agency of frugivorous birds to explain the wide dispersal of this species. The seeds are light in weight and remind one a little of those of the succulent fruits of Freycinetia. For purposes of dispersal, however, they must be placed in the same category with other plants with dry, dehiscent fruits and small seeds, such as the Vota (Geissois ternata) of Fiji, a tree that in those islands grows in similar stations. On a later page I have suggested that the seeds of the Vota are dispersed by large bats that visit the trees for the sake of the honey in the red flowers. With Metrosideros polymorpha birds act probably in the same way. We are, in fact, informed by Mr. Perkins that the nectar-feeding birds of the Hawaiian Drepanids now obtain their main supply of this food from the blossoms of this tree. If bats or birds visit the large red flowers of Metrosideros polymorpha for the same purpose, it is not difficult to imagine that they might carry away in their fur or in their plumage some of the small seeds shaken out of old dehiscent capsules. In this connection we may note

that the Kaka Parrot (Nestor meridionalis) of New Zealand is said to feed largely on the scarlet blossoms and nectar of Metrosideros robusta (Evans' *Birds*, p. 374).

The seeds of Metrosideros polymorpha might no doubt be carried by winds from one mountain-top to another and across narrow straits, but only whilst adherent to a bat or a bird could they be carried across a wide tract of ocean. Speaking of the genera Metrosideros and Lobelia in connection with their occurrence in the Kermadec Islands, Sir J. Hooker long ago referred to their minute seeds as not adapted for transport across oceans unless their minuteness and number fitted them for it (*Journ. Linn. Soc.*, i. 127). The point that is raised here for these genera in the Kermadec Group can be raised for the same two genera in Hawaii and for a multitude of other small-seeded genera in those islands.

Alyxia (Apocynaceæ).

This genus of climbing or straggling shrubs tells its own story of the widely dispersed Indo-Malayan genera in the Pacific islands. Containing about forty known species, it is distributed over the tropical regions from Madagascar and the Mascarene Islands eastward to the Paumotu Group and Pitcairn Island in mid-Pacific, and has its focus in the area comprised by Malaya, Australia, and New Caledonia. In the *Index Kewensis* about eight species are assigned to New Caledonia, seven to Australia, and seven to Malaya. One species, Alyxia stellata, ranges over nearly the whole of the area of the genus from tropical Asia, through Malaya, across the South Pacific to Tahiti. It will be for the future investigator to determine how far the present distribution of the genus can be connected with one or two widely-ranging polymorphous species. The data at my disposal seem to show that in the open Pacific, at all events, the history of the genus has gone a step beyond this stage.

Of the seven or eight species recorded from the Pacific islands east of New Caledonia, only two or three seem to be now recognised as restricted to particular groups, namely, one in Hawaii (Schumann), one in Fiji, and one in Rarotonga. The other species indirectly connect together all the groups, although no single species occurs over the whole region. Thus the Hawaiian species, Alyxia olivæformis (Gaud.) has in recent years been found in Upolu, in the Samoan Group, by Dr. Reinecke, an exceedingly interesting though unusual specific link between these two

archipelagoes. Two species, A. stellata and A. scandens, range over the South Pacific from Fiji to Tahiti, the last-named also occurring in the Paumotu or Low Archipelago; whilst Rarotonga possesses a form closely allied to the first-named, and to it Cheeseman has given specific rank. Another species, A. bracteolosa, links together the contiguous Fijian, Tongan, and Samoan groups. This distribution is what we should have expected if one or two polymorphous species had originally ranged over the Pacific and were advancing towards that stage of differentiation when each group possesses its own peculiar species. (It may be here remarked that an undetermined species of Alyxia is accredited by Maiden to Pitcairn Island, which indicates that the genus has extended east in the Pacific almost as far as the extreme limit of the Polynesian region.—*Australas. Assoc. Reports*, Melb., 1901, viii.)

All visitors to these islands that are interested in their floras will be familiar with the Alyxias; and there are few of their plants that the natives take more pleasure in pointing out to white men. They are readily recognised on account of their black moniliform drupes and their milky sap. All over Polynesia, whether in Hawaii, Tahiti, Samoa, or Fiji, the aborigines value the plants on account of the delicate fragrance of their foliage and bark. These materials they use for personal decoration and in making wreaths, stripping off the bark of the young branches with their teeth in the same fashion in Fiji and Hawaii and probably in all the Pacific islands. Throughout Polynesia, excluding Fiji, they bear the same name, which takes the form of "maile" in Hawaii and Samoa, and of "maire" in Tahiti and Rarotonga—a name which the Maoris, remembering the Alyxias of their tropical home in the South Pacific, have applied to New Zealand species of Olea and Eugenia. The Fijian generic name for Alyxia is "vono."

A word may be said about the station of these plants in the Pacific islands. In Hawaii they occur in the middle and lower forests, and usually between 2,000 and 4,000 feet in elevation. In Tahiti they frequent the crests and precipitous rocky slopes of the mountains at elevations of from 3,000 to over 6,000 feet. The Rarotongan species often forms extensive thickets in rocky localities on the hills. In Samoa they are found usually in the mountain forests. In Fiji they grow on the outskirts of the virgin forests and on rocky sparingly vegetated mountain peaks. I found them often in Vanua Levu growing amongst the open vegetation on the summits of isolated mountains at elevations of 2,000 to 2,500 feet, where they were associated with other plants like

Elæocarpus, Pleiosmilax, and Scævola, possessing similar fleshy fruits likely to be dispersed by frugivorous birds.

The Alyxias indeed seem well suited for dispersal by birds. The black fleshy drupes would readily attract them; and the solitary seed protected by a very tough horny albumen might be ejected unharmed in their droppings.

It would be possible to enter into similar detail with several other genera of this period; but here I can only direct attention to their principal indications, permitting myself a little more license when discussing the means of dispersal.

ALPHITONIA (Rhamnaceæ).—Amongst other genera with polymorphous species closely following the lines taken by Metrosideros in the Pacific is Alphitonia, a small Malayan and Polynesian genus of tall trees, containing at most three or four species, one of which (A. excelsa) has almost the range of the genus and is found in most of the Pacific archipelagoes. So variable is this widely-ranging tree that Bentham suggested that there was only one species in the genus (*Bot. Chall. Exped.*, iii. 133), a suggestion especially interesting in connection with the *rôle* taken by polymorphous species in the Pacific. As bearing on the mode of dispersal of this species, it may be observed that my Fijian experiments show that the fruits are not fit for transport by currents. With the mature drupe the outer coverings become pulverulent, and the fruit breaks down, freeing the pyrenes which do not float; nor have the seeds any buoyancy. Although the dry drupes would seem unattractive to birds, it is to birds we must look for the dispersal of the genus.

PISONIA (Nyctagineæ).—Like Dodonæa, Metrosideros, and Alphitonia, the cosmopolitan genus Pisonia possesses a polymorphous species that displays its variation in every Pacific group and occupies a considerable number of stations. The earlier botanists in the Pacific differed much as to the species of this region, and this led Mr. Hemsley to observe in his paper on the Tongan flora that it is difficult to understand the various Polynesian and Australian species except on the assumption that there is one very variable species. Recognising this difficulty, Drake del Castillo deals somewhat summarily with nearly all these forms, uniting them under one comprehensive species, P. umbellifera (Seem.), thus constituting "une espèce très-polymorphe" that ranges (generally in maritime districts) over tropical Asia and the

islands of the Indian and Pacific Oceans, extending to North-East Australia and to New Zealand. On account of the unusual capacity for dispersal possessed by this species—a subject to be immediately discussed—the tendency to specific differentiation has been kept in check, though the process has gone farther in some groups than in others, as in the case of Hawaii, where Hillebrand's endemic species has, however, been included by Drake del Castillo in his polymorphous species, P. umbellifera.

The fruits of this genus possess no capacity for dispersal by currents. They never came under my notice either in floating or stranded seed-drift, and have little or no buoyancy. Prof. Schimper, experimenting on the well-dried fruits of Pisonia aculeata, a seaside shrub common in America and in the Old World, and destined probably to be brought by the systematist into touch with the polymorphous P. umbellifera, found that they sank in a day or two (*Ind. Mal. Strand-flora*, p. 156). Dismissing the agency of the current, he looked to that of the bird for the explanation of the dispersal. The probability of the effectiveness of this last-named agency has long been surmised. It attracted the notice of Darwin and especially invited the attention of another student of plant-dispersal, Dr. H. O. Forbes. The long, narrow, often fusiform fruits are invested by a somewhat coriaceous perigone and range from less than an inch to three inches in length (2—7·5 cm.). They excrete a very viscid fluid often in quantity, and sometimes also possess glandular spines. The Hawaiians, according to Hillebrand, used this material as bird-lime for catching birds, and the fruits, he says, will stick fast to the paper in the herbarium for years. In that group I often found the fruit adhering firmly to my clothes. Writing of these trees on Keeling Atoll, Forbes observes that their sticky fruits are often such a pest to birds roosting in their branches that they have proved fatal to herons and boobies by collecting in their plumage. "It is easy to perceive," he remarks, "how widely this tree might be disseminated by the birds that roost on it" (*The Eastern Archipelago*, p. 30). In New Zealand, as we learn from Kirk, the viscid fruits of Pisonia brunoniana attract small birds which become firmly caught and die miserably. A cat has been known to wait under a tree watching its opportunity of preying on the entangled birds. Sir W. Buller states that the New Zealand fruit-pigeon feeds at times on the green fruits of P. umbellifera; and we can infer that it occasionally carries off some of the riper fruits in its feathers.

WIKSTRŒMIA (Thymelæaceæ).—This is a small genus of shrubs and small trees, with red or yellowish drupes fitted for dispersal by frugivorous birds, that is confined mainly to tropical Asia, Australia, and Polynesia. Following Seemann and Drake del Castillo, we may say, that like several other genera of this period, this genus possesses in the tropical Pacific a widely-ranging species, W. indica, that occurs in Hawaii, the Marquesas, Tahiti, Samoa, and Fiji, growing amongst the vegetation immediately behind the beaches and in the plains and open wooded districts inland. In Hawaii it is associated with half a dozen peculiar species, and in Tonga there is also an endemic species. The widely-ranging species has its home in the Indian Archipelago and in the Asiatic mainland, and occurs also in Australia. According to Gray, the American botanist, it is represented by a different variety in almost every group in the tropical Pacific, and it presents us therefore with another example of a polymorphous species which links Polynesia directly with Malaya. As bearing on the dispersal of the genus by birds, it may be added that Mr. Perkins in the *Fauna Hawaiiensis* speaks of some of the Drepanids and of a species of Phaeornis as feeding at times on the fruits of these plants.

PEPEROMIA (Piperaceæ).—All observers of tropical plant-life will be familiar with this genus of low herbs growing on tree-trunks, on the soil, on rocks, and on stonewalls, and comprising about 500 known species distributed over the warmer regions of the globe and sometimes extending into cooler latitudes. In Polynesia it attains its greatest development in Hawaii, where Hillebrand enumerates about twenty species, of which, after excluding doubtful forms, at least a third must be endemic. Tahiti, Samoa, and Fiji are each known to possess three or four species, of which one is usually restricted to the group. Two species, P. reflexa and P. leptostachya, link together nearly all the groups of the tropical Pacific, including Hawaii, the first cosmopolitan, and the second hailing from North-East Australia and indicating that the genus has entered Polynesia from the west. . . . These plants possess spikes of small berries containing a single seed, and are evidently, like other Piperaceæ, dispersed by frugivorous birds. It is to be noted that the presence of a West Indian and Mexican species in the Bermudian caves is attributed by Mr. Hemsley to frugivorous birds (*Bot. Chall. Exped.*, Introd. 49, i. 62). In Vanua Levu they occur on the bare rocky peaks of some of the mountains under such conditions that the seeds could only have

been brought by birds. Thus, on the bare surface of a large block of tuff forming the highest peak of Koro-Mbasanga, 2,500 feet above the sea, I found only two plants, Oxalis corniculata and a species of Peperomia.

EUGENIA (Myrtaceæ).—This is a very extensive genus split up into different subgenera, and comprising some 600 or 700 known species scattered over the warm regions of the globe. Their fleshy, usually red, berries contain as a rule one or two large seeds, and attract birds and animals of all descriptions. The feature most interesting to us is the dispersal of the genus over the Pacific islands eastward to the Low Archipelago and northward to Hawaii. The track by which it has entered the Pacific from the west is indicated in the distribution of the species. The genus is only well represented in the Western Pacific, whilst eastward and northward of Samoa and Tonga the distribution is fitful and irregular, it being evident that the extension beyond these two groups has been accomplished with difficulty.

There are at least twenty-five species in Fiji, of which perhaps half would be peculiar; in Tonga eight species, of which two may be endemic; in Samoa thirteen species, of which four are peculiar; in Rarotonga none; in Tahiti a single non-endemic species; and in Hawaii two species, of which one is peculiar. Only truly indigenous species are here recorded, and Eugenia malaccensis, which has accompanied the aborigines in their migrations, is not included. A solitary species, E. rariflora, connects together all the principal archipelagoes from Fiji to Tahiti and the Gambier Islands, and northward to Hawaii. Nine species are known to be common to the region in which lie the three groups of Fiji, Tonga, and Samoa; and since some of these species occur in the groups further west they may be regarded as keeping up the connection with the original home of their ancestors in the Malayan region.

Looking at these facts of distribution of the genus Eugenia in the open Pacific, it is evident that whatever dispersal of the genus is now in progress in this ocean is mainly confined to an interchange between the groups of Fiji, Tonga, and Samoa in the Western Pacific, and doubtless between the islands further west of these groups. The smaller islands lying between and around these three groups participate in the distribution of the species common to all. Thus Wallis Island, according to Drake del Castillo, possesses two of these species. Over the rest of the ocean the dispersal of the genus seems to be no longer effective, since Eugenia rariflora, which links together Fiji, Tahiti,

and Hawaii, shows signs of differentiation in nearly every group. In Hawaii, where it is very rare and is only recorded from two of the islands, it has developed a small-leaved variety. In Tahiti it displays the same variation; and Seemann observes that there are differences between the Tahitian and Fijian species which may be almost specific in value. It would also appear that both in Hawaii and Tahiti the fruits have become less attractive to birds, being described as "dryish" and "dry," which is, as Dr. Seemann remarks, certainly not true of the Fijian plant.

In Fiji the Eugenias, as small trees and shrubs, find their home usually on the banks of streams and rivers, on the outskirts of forests, and occasionally at the coast. One of them, E. richii (Gray), is a characteristic littoral tree in the group. A tree near it in character was found by me of common occurrence in the interior of coral islets in the Solomon Group (*Solomon Islands*, p. 297). E. rariflora occurs also in the interior of coral islets in Fiji and amongst the vegetation at the back of the mangrove-swamps.

Coming to the mode of dispersal of the genus in the Pacific, I may remark that all the species, with the doubtful exception of the Fijian and Samoan Eugenia neurocalyx (the Lemba of Fiji), are wild trees and shrubs useless to man, but much appreciated by pigeons, pigs, &c., on account of their fleshy fruits. Since exact observations on the possibility of their dispersal by currents seemed to be wanting, I made some experiments in Fiji. Out of six species, which included E. corynocarpa, rariflora, richii, and rivularis, the mature fruits of most species sank in sea-water in from seven to ten days. However, those of the beach tree, E. richii, floated for a fortnight. The cause of sinking in all cases lay in the decay of the outer fleshy covering. As I have observed in river and sea drift, fish bite at the floating fruits, and in this manner the seeds would soon be liberated and sink. The seeds of all the plants sank at once in my experiments except with one species, where the seed loosely filled its test and thus a floating-power of a few days was acquired. Currents, it is apparent, could never account for the dispersal of the genus over a broad extent of ocean, though in a few cases, as in that of the littoral tree above noted, it is quite possible that the fruits could be successfully transported across a tract of sea 200 or 300 miles in width.

It has long been known that fruit-pigeons are fond of the fruits of wild species of Eugenia, and I found the Solomon Islanders and the Fijians well acquainted with the fact. The fruits of a tall Eugenia tree, near E. richii, common in the interior of the

coral islets of Bougainville Straits in the Solomon Group, were found by me in quantities in the crops of fruit-pigeons shot by Lieut. Heming and Lieut. Leeper on the islets (*Solomon Islands*, pp. 293, 297; *Bot. Chall. Exped.*, Introd. 46, iv. 312). Dr. Seemann remarks that in Fiji the red fruits of E. brackenridgei are eaten by pigeons. The somewhat thin coverings of the seeds of this genus would seem to offer but a slight protection in a bird's stomach, though in one species the test was almost crustaceous.

Most species possessed only one or two large seeds in each fruit, though this number may vary in the same individual. Thus, out of ten fruits of Eugenia rariflora in Fiji, six had one seed, three had two seeds, and one had three seeds. In the fruit of E. neurocalyx, however, the seeds range from three to five.

It is the question of size that is of importance in considering the possibility of birds transporting the seeds over a broad tract of ocean. Eugenia rariflora, the species found all over the Pacific, has seeds that measure in the Fijian plant one-fourth to one-third of an inch (6 to 8 mm.) across; and in Hawaii, according to Hillebrand, they would perhaps be rather smaller. In point of size there is less difficulty with regard to the transport by birds across the ocean to Hawaii of the seeds of Eugenia rariflora than with the "stones" and seeds of some other genera, like Elæocarpus, Osmanthus, and Sideroxylon, that must have been conveyed there by the same agency. The fruits of several of the Fijian species are of the size of a large cherry; but it is noteworthy that in those species like E. corynocarpa and E. neurocalyx, where the fruits are large and the seeds about an inch in size, the plants are confined to the Western Pacific only, namely, to the Fiji-Samoa region.

There is therefore no difficulty, from the standpoint of size, in accounting for the distribution by birds of the widely-ranging Eugenia rariflora over Polynesia; but at first sight there seems to be a real difficulty with regard to the protective coverings of the seed. Yet Nature speaks with no hesitating voice in the matter. The West Indian and Florida species, E. monticola, regarded as indigenous in the Bermudas, must have reached that group through the agency of birds that carried its seeds over quite 800 or 900 miles of sea; and it may here be noted that South Trinidad, lying some 600 miles off the coast of Brazil, and Rodriguez, distant about 330 miles from Mauritius, each possess species (*Bot. Chall. Exped.*, Introd., 12, i. 32, ii. 128). If fruit-pigeons can transport Eugenia seeds across 600 or 800 miles of ocean, there would be no difficulty in accounting for the stocking of the Fijian, Tongan,

and Samoan Islands with the genus from regions to the west. But the occurrence of the genus in Hawaii seems to compel us to assume that the seeds have been carried in a bird's stomach over 1,500 to 2,000 miles of ocean. This difficulty, however, does not really exist. Eugenia rariflora, the Polynesian species found in Hawaii, frequents, as before observed, coast districts and coral islets in Fiji, and if we suppose that the low islands of the Fanning and Phœnix Groups, lying between Hawaii and Samoa, have served as stepping-stones, a capacity of crossing 1,000 miles of ocean would be alone required. This is not much in excess of the distance that must have been traversed by the bird that first brought the seeds of Eugenia monticola to the Bermudas.

Other genera like Morinda and Scævola, possessing fleshy fruits dispersed by frugivorous birds, have been mentioned in different connections in other parts of this work, and will not be further dealt with here. But before concluding this chapter I will refer briefly to one of the disquieting mysteries in the flora of the Pacific which is presented to us in the genus Gossypium. Three species are, or were, truly indigenous in this region. One is Gossypium drynarioides, a small endemic tree found by Nelson, the companion of Captain Cook, in Hawaii, which was very rare in Hillebrand's time, and is perhaps now extinct. The second is G. tomentosum (Nuttall), which is also peculiar to Hawaii, where it is found on the beaches. I am following here the *Index Kewensis*; but it should be remarked that this species occurs also in Fiji, though Seemann regards it as introduced. The third is G. religiosum (L.), found by Captain Cook's botanists growing wild in Tahiti, and hailing from the tropics of the Old World. The seeds of the first species are covered with a short brownish tomentum, and could never have been of any value. The tawny wool of the seeds of the second species has a staple too short for cultivation; whilst the Tahitians do not seem to have made any use of the third species. It is difficult to draw any conclusion concerning the presence of these plants in the Pacific islands at the time of their discovery; nor can Dr. Seemann, who was especially well informed in these matters, aid us much in our endeavours to solve the mystery. From the aboriginal names we get no clue. The Hawaiian name of "huluhulu" seemingly refers to the hairy covering of the seed; whilst the Tahitian "vavai" and "ovari" simulate the Fijian "vauvau," which is merely the reduplicated form of "vau" (the word in many shapes for Hibiscus tiliaceus in Malaya and Poly-

nesia), and is applied by the Fijians to Hibiscus esculentus and to the introduced species of Gossypium.

When in Hawaii I ascertained that neither the seeds of the littoral plant, Gossypium tomentosum, nor those of two cultivated species possessed any fitness for dispersal by the currents, the scraped seeds sinking at once, whilst when covered with the wool they floated only for a few days. Further references to G. tomentosum in Hawaii are given in the index of this volume.

The Last Stage of the General Dispersal of Plants of the Malayan Era.

We arrive now at the close of the era of the general dispersal of tropical plants, mainly Malayan, over the Pacific, and this brings us down to our own age. The few genera that are still dispersed have no peculiar species in particular groups. The species which often range over all the groups, and retain as a rule their characters in most of them, do not therefore display, except in a few cases, that extreme variation which would give them a place in the ranks of the polymorphous species. The dispersing agencies, in fact, are sufficiently active to check marked variations, and the process of isolation has scarcely begun.

We perceive the reason of this when we look at the nine genera which are taken as samples of this period, viz., Rhus, Osteomeles, Viscum, Plectronia, Boerhaavia, Polygonum, Pipturus, Boehmeria, and Dianella, most of them being known to be dispersed by birds at the present day. Six of the genera possess fruits likely to attract frugivorous birds; whilst one of them, Boerhaavia, has sticky fruits that would be apt to adhere to plumage. Actual observations in the cases of Rhus, Viscum, and Plectronia establish the fact of their dispersal by fruit-eating birds; and there is no difficulty in postulating the same agency for Osteomeles, Pipturus, and Dianella. A method by which Boerhaavia fruits would be transported in the plumage of birds has been observed by Mr. Lister; whilst the nutlets of Polygonum are known to afford food to a variety of birds and to be thus distributed.

In this period the plants all hail from the Asiatic side of the Pacific. Three of the genera, Plectronia, Pipturus, and Dianella, belong almost exclusively to the Old World. Five occur in both the Old and New Worlds, but, as with Rhus, Viscum, Boerhaavia, and Bœhmeria, are represented by Old World species in the Pacific,

or, as with Polygonum, possess a cosmopolitan species (P. glabrum) ranging over the warm regions of the globe. Even Osteomeles presents no exception to the rule, since the Pacific plant is the only one of its species that is not American.

We have in Polygonum glabrum the only aquatic or semi-aquatic plant widely distributed over the Pacific islands that can lay claim in all groups to be indigenous. It is associated in Hawaii with species of Potamogeton and Naias, aquatic genera that have, however, a limited distribution in Polynesia.

I will now make a few remarks on each genus such as bear on their distribution and on their mode of dispersal in the Pacific.

RHUS (Anacardiaceæ).—The representation of this genus by indigenous species in oceanic islands not only in the Pacific but also in the Atlantic, as in the Bermudas, is of especial interest in connection with dispersal by frugivorous birds, since the drupes are typically dryish and might appear to be not very attractive to birds. There are two Old World species known from the Pacific islands: one being R. simarubæfolia (Gray), distributed over the South Pacific groups from Fiji to Tahiti and hailing from Malaya; the other, R. semialata (Murray), alone recorded from the Hawaiian Group and derived probably from China or Japan. This indication that the groups of the North and South Pacific have derived their species, the first from Temperate Asia and the second from Tropical Asia, is of some interest. In Samoa, according to Reinecke, the fruits of R. simarubæfolia, which are of the size of a pea, form the favourite food of the fruit-pigeons. That birds disperse the seeds of the various Sumachs is familiarly known. In the United States, as we learn from Barrows, Beal, and Weed, crows, woodpeckers, and other birds feed extensively in winter on the fruits of different species of Rhus, including the Poison Ivy (R. toxicodendron). The crows discharge the seeds in pellets after retaining them for about thirty minutes. Some seeds we must infer would pass into the intestines, where they might be retained for ten to twelve hours (see Chapter XXXIII.), which would be long enough, according to Gätke's views of bird-velocity, to enable them to be transported over a thousand miles of ocean.

OSTEOMELES (Rosaceæ).—One of the most interesting cases of dispersal in recent times over the Pacific islands is that of O. anthyllidifolia. Of the ten known species of the genus, nine are confined to South America; whilst the Pacific species, which is not recorded from America, has been found in Upper Burma, Japan, the Liukiu and Bonin Groups, Hawaii, Pitcairn Island,

Mangaia, and Rarotonga. The remarkable distribution of the Pacific plant at once attracts attention. I was very familiar with it in Hawaii, where it forms one of the commonest bushes in open-wooded and thinly vegetated districts at elevations usually ranging from the coast to 3,000 feet. Its small, white, somewhat fleshy fruits would attract birds, and the hard pyrenes would be able to pass unharmed through a bird's digestive canal. It seems probable that, like Rhus semialata, this plant entered the Pacific Ocean from the north-west, taking the route by Japan and the Bonin Islands, and following the trend of the archipelagoes over Polynesia (see *Bot. Chall. Exped.*, Introd. p. 18; *Journ. Linn. Soc. Bot.*, vol. 28, 1891, &c.).

VISCUM (Loranthaceæ).—A single species, V. articulatum, which has its home in Southern Asia, is found in most of the Pacific groups, such as Hawaii, Marquesas, Tahiti, Rarotonga, Fiji, &c. The dispersal of the genus by frugivorous birds is well known.

PLECTRONIA (Rubiaceæ).—I have found it more convenient to place this genus here, although there are probably one or two species peculiar to Fiji. This genus of shrubs, which is spread over the warm regions of the Old World, is represented by two widely distributed species in Polynesia, Plectronia odorata (B. and H.) and P. barbata (B. and H.), the first alone extending to Hawaii. I was very familiar with P. odorata in Hawaii and was much interested in its mode of dispersal, since the species has also been found in Fiji, Tahiti, the Marquesas, and Pitcairn Island (Maiden). In one locality, where an old lava-field was partially covered by its bushes then in fruit, the doves were feeding greedily on the drupes, the "stones" of which, as well as the partially digested fruits, were to be seen in quantity in their excrement near a water-hole. The stones are very hard and about a third of an inch (8 mm.) in length, and are exceedingly well suited for transport by frugivorous birds. It was very probably to one of these species of Plectronia that Peale alluded when he wrote of the berries of a species of Canthium forming the principal food, on one of the Paumotu Islands, of Numenius tahitensis, a curlew that has its home in Alaska, migrating south in autumn to Hawaii, Tahiti, and the Paumotu Group (Wilson's *Aves Hawaiienses*).

BOERHAAVIA (Nyctagineæ).—Two or three Asiatic species oı this genus, B. diffusa, B. tetranda, &c., are spread all over the Pacific islands from the Fijis to the Paumotus and northward to Hawaii. Similar or allied species occur on the coral islands of the Indian Ocean, as on Diego Garcia and on Keeling Atoll. Though

these plants have often been accidentally spread by man with his cultivated plants, it is probable that sea-birds have regularly aided in their dispersal. The fruits, on account of their small size and their glutinous sticky surfaces, are well suited for transport in a bird's feathers. Mr. Lister, as quoted by Hedley (from *Proc. Zoolog. Soc.*, 1891), made an interesting note in this connection on one of the islands of the Phœnix Group, where he found a fruit of Boerhaavia tetrandra entangled in some of the down that had been preened by a booby (Sula piscatrix) out of its feathers whilst roosting in a clump of Tournefortia trees.

POLYGONUM (Polygonaceæ).—This genus is represented by the cosmopolitan Polygonum glabrum, the only aquatic or semi-aquatic plant that is generally distributed in the Pacific islands. It occurs in fresh-water swamps and beside streams and ponds in Tahiti, Tonga, Fiji, Hawaii, &c., and was gathered by Banks and Solander when Captain Cook first visited Tahiti. That this plant has been distributed by geese, ducks, and waterfowl over the tropics of the globe can scarcely be doubted. In England I have found the nutlets of Polygonum convolvulus, P. persicaria, and P. aviculare in the stomachs of a wild duck and a curlew; and they came frequently under my notice in the crops and intestines of different kinds of partridges and of wood-pigeons. Though most of the fruits were generally injured, a few of them were not uncommonly obtained in a sound condition.

PIPTURUS (Urticaceæ).—This is a genus of small trees and shrubs found in the Mascarene Islands, Malaya, Australia, New Zealand, and throughout Polynesia. Besides P. albidus, which is confined to Hawaii and Tahiti, there are two Malayan species, P. argenteus and P. velutinus, which are widely distributed over the islands of the South Pacific, extending to Tahiti and the Marquesas. The fleshy receptacle and small achenes of the compound fruit of Pipturus give it the appearance of a white immature strawberry, and as such it would be likely to attract frugivorous birds. Plants of this genus are included amongst the numerous plants from the bast of which the natives used to prepare their native cloth or from which they obtained the fibres for their fishing-lines.

BŒHMERIA (Urticaceæ).—There is an Asiatic species widely spread in the South Pacific and another closely-allied species in Hawaii; but I possess no data relating to the dispersal of the genus. The fruits are dry and consist of an achene in a persistent perianth.

DIANELLA (Liliaceæ).—This is a genus of herbs, possessing

often pretty blue berries, that extends over tropical Africa, tropical Asia, the Mascarene Islands, Malaya, Australia, and New Zealand, and is found in all the larger Pacific archipelagoes. Of the twelve species named in the *Index Kewensis* only two belong to America, occurring respectively in Cuba and Venezuela. There are two species in the islands of the tropical Pacific: (*a*) Dianella ensifolia, found in Hawaii and ranging over the Mascarene Islands, India, China, Malaya, and tropical Australia; and (*b*) D. intermedia, recorded from most of the groups of the South Pacific (Fiji, Tonga, Rarotonga, Tahiti), and occurring also in Norfolk Island and New Zealand. These two plants occur in similar stations all over Polynesia, sometimes growing in the grassy plains on the dry side of an island, at other times extending up the thinly wooded mountain slopes and reaching the hill-crests some 2,000 or 3,000 feet above the sea. Their berries would readily attract birds; and their seeds, about one-fifth of an inch (5 mm.) in size in the case of D. ensifolia, could be carried uninjured in the stomach and intestines of a bird.

Summary.

(1) A later period in the era of the general dispersal of Malayan plants over the Pacific is indicated by the genera that contain species found outside each group as well as species restricted to it.

(2) In this period the extremely variable or polymorphous species plays a conspicuous part, as represented in such genera as Alphitonia, Dodonæa, Metrosideros, Pisonia, and Wikstrœmia.

(3) The first stage is displayed by a solitary widely-ranging species found over most of the Polynesian archipelagoes, and varying independently in every group.

(4) The next stage is shown where the polymorphous species, having done its work of distributing the genus, ceases to wander and settles down and "differentiates" in all the groups; and the genus thus includes both peculiar and widely-ranging species in each group. Most of the genera possessing polymorphous species are in this stage.

(5) The following stage is displayed by those genera like Elæocarpus, Eugenia, and Peperomia, where peculiar species are especially developed in particular groups, and we get subcentres of distribution for the genus, that is to say, small gatherings of

peculiar species. A few species, however, still keep up a connection with neighbouring island-groups. Should this be severed we get the type of genus belonging to the earlier period of the Malayan era as described in the preceding chapter, a genus possessing only peculiar species and destined, after ages of further isolation through the failure of the dispersing agencies, to give rise to a new generic type or types.

(6) Frugivorous birds were chiefly active in dispersing these genera over the Pacific. Some of the genera possess seeds or "stones" of such a size that at first sight their transport by frugivorous birds to Hawaii seems improbable; but, as in the case of Elæocarpus, it is shown that this difficulty does not apply to all species of a genus, some of them having much smaller seeds or stones.

(7) The close of the era of the general dispersal of Malayan plants over the Polynesian Islands is indicated by those genera that are represented more or less entirely by widely ranging species. Though such species may vary among the different groups, they rarely take the rank of polymorphous species, the agencies of dispersal being sufficiently active to check marked variations.

(8) Several of the genera of this concluding stage, like Rhus, Viscum, and Plectronia, are known to be dispersed by frugivorous birds, whilst others, like Osteomeles and Dianella, are equally well suited for this mode of dispersal.

(9) Distinct indications are afforded by the genera Rhus, Osteomeles, and Dianella that the Hawaiian Group has been often supplied with its plants directly from the Old World by the Asiatic mainland, whilst the groups of the South Pacific have received different species of the same genus by Malaya and tropical Australia.

CHAPTER XXVII

THE MALAYAN ERA OF THE NON-ENDEMIC GENERA OF FLOWERING PLANTS (*continued*)

THE AGE OF LOCAL DISPERSAL

Synopsis of the Chapter.

HAWAII.—(1) *The Hawaiian residual genera, being those not found in either the Fijian or the Tahitian regions.* The genera especially discussed are Osmanthus, Sicyos, Jacquemontia, Cuscuta, Rumex, Dracæna, Naias, Potamogeton ; and amongst others mentioned are Perrottetia and Embelia.

(2) *The Hawaiian genera found in Tahiti and not in Fiji.* Very few, and illustrated by Byronia, Reynoldsia or Trevesia, Phyllostegia, and Pseudomorus, though it is likely that most of these will be subsequently discovered in Fiji.

(3) *The Hawaiian genera found in Fiji and not in Tahiti.* Illustrated by Eurya, Gouania, Maba, Sideroxylon, Antidesma, Pleiosmilax, Ruppia.

(4) *The absentees from Hawaii.* Illustrated amongst the orders by the Sterculiaceæ (see text), the Meliaceæ, the Rhizophoreæ, the Melastomaceæ, and the Coniferæ, and amongst the genera by Trichospermum Loranthus, Stylocoryne, Ophiorrhiza, Alstonia, Hoya, Ficus ; and a great many others might be cited.

TAHITI.—(1) *The Tahitian residual genera.* Only six in number—Cratæva, Buettneria, Berrya, Coriaria, Bidens, Lepinia.

(2) *The Tahitian genera found in Hawaii and not in Fiji.* See above under (2).

(3) *The Tahitian genera found in Fiji and not in Hawaii.* (a) Those possessing only species confined to the Tahitian region or to East Polynesia, of which Meryta, Ophiorrhiza, Alstonia, and Loranthus are examples.

(b) Those possessing widely-ranging species besides, often, species confined to the Tahitian region, such as Grewia, Nelitris, Melastoma, Randia Geniostoma, Tabernæmontana, Fagræa, Bischoffia, Macaranga, and Ficus. The widely-ranging species is in many genera polymorphous.

(4) *The absentees from Tahiti.* Amongst the orders are the Meliaceæ, the Rhizophoreæ, and the Coniferæ. Amongst the genera, usually those with "stones" or large seeds an inch in size, such as Canarium, Dracontomelon, Myristica, Sterculia, Veitchia, &c. Numerous other absent genera might be named.

FIJI.—*The Fijian genera not found either in Tahiti or Hawaii.* These genera compose about half the Fijian flora, being at least 160 in number. Those especially discussed here are the following:—Hibbertia, Cananga, Sterculia, Trichospermum, Micromelum, Canarium, Dracontomelon, Begonia, Geissois, Dolicholobium, Lindenia, Myrmecodia, Hydnophytum, Couthovia, Limnanthemum, Myristica, Elatostema, Ceratophyllum, Gnetum, Veitchia, Rhaphidophora, Lemna, Wolffia, Scirpodendron. The Coniferæ are dealt with in Chapter XXIV.

Note appended on Marsilea.

HAVING completed our discussion of the general dispersal of tropical genera, chiefly Indo-Malayan, over the Pacific islands, we pass on now to consider the more restricted distribution of non-endemic genera over this region. Here as before we take Hawaii, Tahiti, and Fiji as the three centres of distribution; and here also we deal with the flowering plants after excluding the orchids, the sedges, the grasses, the mountain-plants, and all plants introduced either by the aborigines or by white men.

HAWAII.

After excluding the endemic genera as well as those that are confined to the mountains, we find that this group possesses very few genera that do not occur in the Fijian and Tahitian regions, and fewer still that it owns in common with Tahiti to the exclusion of Fiji. On the other hand, we observe that Fiji possesses a great number of genera, mostly Asiatic in origin, that have not reached Hawaii, and in several cases are not known, from the Tahitian region. These contrasts might have been expected, since the Pacific islands have in later ages been mainly stocked from the Asiatic side of the Pacific, the principal route lying through the Fijian region.

As far as the flora of the lower levels (below 4,000 feet) is concerned, Hawaii only possesses a portion of that which Fiji has derived from the Old World, chiefly through Malaya. Although, as will be shown below, there is a noticeable contribution from America, it is very far from counterbalancing the loss which the Hawaiian flora has sustained in comparison with Fiji through

the isolated position of the group. The want of variety, however, in the flora of the Hawaiian lower levels, which up to 4,000 or 5,000 feet represent the islands of the less elevated Fijian region, is in a small degree compensated for by the development of new genera and new species and by the great number of individuals. Trees like Metrosideros polymorpha and Aleurites moluccana, that in the southern groups form only one of many contributors to the forests, rise suddenly into prominence in the northern archipelago and form entire forests. Pandanus odoratissimus largely composes extensive forests in the province of Puna in the large island of Hawaii, extending several miles inland and nearly 2,000 feet up the mountain slopes.

The remarkable contrast between the Fijian flora, which is almost entirely tropical, and the Hawaiian flora, which on account of the great elevation of the islands is temperate as well as tropical, is brought into yet greater prominence when we look at it more closely and treat it numerically. The Hawaiian Group, it must be first observed, though possessing the same area as Fiji and presenting a far greater variety of climatic conditions, has only two-thirds the number of genera of flowering plants (see Chapter XXI., Table B). Whilst at least 200 of the Fijian genera of indigenous plants (excluding the orchids and the grasses) are not found in Hawaii, only about 100 of the Hawaiian genera are absent from Fiji, and the two groups possess about 100 genera in common. When we look more closely at the hundred Hawaiian genera not found in Fiji, we find that about sixty represent endemic genera (thirty-seven) and non-endemic mountain-genera (twenty-two), which naturally are not to be found in Fiji, so that there remain but a small number of genera distinguishing the tropical flora of Hawaii from the Fijian flora. When we take from them a few that occur in the Tahitian region, there is left a very small residuum characteristic of Hawaii alone to the exclusion of the Fijian and Tahitian regions of the South Pacific.

The Hawaiian Residual Genera.

It is my purpose now to deal in an illustrative fashion with this Hawaiian residual flora which is composed, as above explained, of the non-endemic tropical genera that are not represented in the Fijian and Tahitian regions. Up to the present we have been dealing with the characters that the floras of Fiji, Tahiti, and Hawaii possess in common as far as tropical genera are concerned.

We will now proceed to discuss their differences in this respect, and will begin with the residual Hawaiian flora.

After eliminating two or three genera that will probably be found in Fiji, but including one or two others that are best treated under the endemic genera, about twenty-seven present themselves for our purpose. Nearly all of them possess only endemic species, and belong therefore to an age of dispersal that has passed away. These residual genera plainly indicate that although Hawaii largely received its flora during the age of general dispersal of Old World genera over the Pacific, it was at the same time independently stocked with plants from other sources. They include among others—Cocculus (4), Cleome (1), *Perrottetia* (1), Mezoneuron (1), *Lythrum*, *Sicyos* (8), Peucedanum (2), Campylotheca (12), Senecio (2), Lobelia (5), Embelia (1), *Chrysophyllum* (1), Rauwolfia (1), *Nama* (1), Osmanthus (1), *Jacquemontia* (1), Breweria (1), Cuscuta (1), Lycium (1), *Sphacele* (1), *Phytolacca*, Rumex (2), *Urera* (2), Pilea, Dracæna (1), Naias, Potamogeton. Those printed in italics are regarded as derived from America; whilst the figures in brackets indicate the number of endemic species, nearly all of the genera except the five above indicated possessing only peculiar species, and these five (Lythrum, Phytolacca, Pilea, Naias, Potamogeton) are only represented by species found outside the group.

American genera form a more conspicuous element than they do amongst the genera that have been generally dispersed over the Pacific, those exclusively American being fairly represented, making a third of the whole. We find, for instance, in the Hawaiian "Olomea," Perrottetia sandwicensis, a small tree that represents in the woods of all the islands the Perrottetias of Mexico and the Andes; whilst with some of those genera that, like Sicyos and Urera, are at home in both the Old and New Worlds, we obtain indications of America being the source of the Hawaiian plants. A few genera again, like Lythrum and Phytolacca, are represented in Hawaii by American species.

Plants with drupes, berries, or other fleshy fruits likely to attract frugivorous birds compose about a third of the total number of these residual genera, whilst fruits or seeds, that were in all probability originally brought entangled in a bird's feathers, are represented by Sicyos. Some of the genera with stone fruits, such as Osmanthus, to which belongs the Hawaiian Olive, present special difficulties on account of the size of the stone, in this case two-thirds of an inch in length. There are also a number of genera with large dry fruits and sometimes large seeds, of which the

method of dispersal is not easy to discover. Thus, Mezoneuron, a Leguminous genus with seeds an inch across (2·5 cm.), and Peucedanum, of the Umbelliferæ, with mericarps half to three-quarters of an inch (1·2 to 1·8 cm.) in length, offer serious difficulties to the student of plant-dispersal. In discussing the difficulty connected with Mezoneuron (see Chapter XV.) he will keep in view the possibility that the original species may have been a littoral plant possessing seeds dispersed by the currents, seeds that lost their buoyancy when the plant established itself inland, just as is now taking place with Afzelia bijuga, a Leguminous littoral tree of Fiji (see Chapter XVII.).

He will also find much to puzzle him in the mode of dispersal of the Hawaiian residual genera of the Convolvulaceæ (Breweria, Jacquemontia, and Cuscuta) that possess only endemic species, and he will speculate as to the manner in which seeds that would seem to possess but little attraction for birds and have no capacity for transportation by the currents could ever have reached these islands, and he will ask himself why it is that the agencies of dispersal, whatever they are, have now ceased to be active. He will perhaps see a way out of his difficulties when he perceives that if isolation has led to the development of peculiar species in Hawaii, it has strangely enough in the case of the Myrsinaceous genus Embelia produced the same effect over the whole range of the genus, and that Hawaii has in this respect derived no advantage from being an oceanic group. According to Carl Mez, nearly all the ninety species of this Old World genus are restricted in their areas, whether continental or insular ("Myrsinaceæ," *Das Pflanzenreich*, 1902); and indeed we do not seem justified in assuming that the isolating influences in the case of this genus have been more effective in Hawaii in the mid-Pacific, or in Mauritius in the Indian Ocean, than they have been in continental regions like the Deccan and Nyassa Land, in all of which localities endemic species occur.

The remarkable development of the Cucurbitaceous genus Sicyos, in Hawaii alone of all the tropical Pacific groups, will attract his attention, and he will find here another instance of that predominant principle in the distribution of Pacific plants, where in a widely-ranging genus we find one of its species covering most of its area, whilst the other species are more or less localised. He will wonder at the limitation to Hawaii of a genus like Dracæna, that is so well adapted for dispersal over the Pacific by frugivorous birds; and in endeavouring to explain the presence in the Hawaiian forests of the gigantic Rumex, R. giganteus, he will

remember that the small group of Tristan da Cunha, equally isolated in the South Atlantic, possesses an endemic species of the same genus. He will discover in the recognised dispersing agencies of wild ducks and other waterfowl an explanation of the occurrence in Hawaii of the aquatic genera Naias and Potamogeton; but he will be puzzled at their restriction to this group alone of the three tropical Pacific archipelagoes here especially discussed.

Amidst these various perplexities he will probably look with relief on the appearance of Phytolacca brachystachys, an endemic species of the American "pokeweeds"; and he will feel grateful to the American botanists like Professor Weed when they tell him that in the United States crows, blackbirds, and other birds successfully disperse these plants, the seeds of which are sometimes able to pass through the alimentary canal undigested.

But by far the most significant lesson that the student of distribution will carry away from his study of the Hawaiian residual genera will be that which he learns from the genera Embelia and Naias. He perceives here that not only with a typical land-genus has specific differentiation occurred to much the same extent in the continental and insular localities of its range, but that even with a typical genus of submerged aquatic plants, where the conditions of existence are as uniform as they are varied in the case of land plants, the process of differentiation has proceeded on the same broad lines in the interior of a continent and in an island in mid-ocean.

The following notes on some of the residual genera refer more particularly to matters connected with distribution and dispersal.

Osmanthus (Oleaceæ).—This genus, according to the *Index Kewensis*, contains six species localised in their several habitats of North America, Hawaii, Japan (two), Hongkong, and the Himalayas. Its representative in this group is the Hawaiian Olive, the Olea sandwicensis of Gray, a prevailing tree in the lower and middle woods (1,000 to 4,000 feet) of all the islands, which, like other Hawaiian plants, such as those of the genera Eurya and Antidesma, indicates that the group has been sometimes independently stocked from the regions of the northern hemisphere. The drupe of this tree contains a stone two-thirds of an inch (17 mm.) in length, and suitable for dispersal by frugivorous birds; and birds have evidently distributed the tree all over the group. In fact Mr. Perkins in mentioning the favourite food of birds of the Hawaiian genus, Phaeornis, refers to the fruits of this tree as well as of the Opiko (Straussia) and of the Olapa (Cheirodendron).

When, however, we come to consider the feasibility of the stones of the genus having been thus originally carried to Hawaii either from Japan or from North America, we meet with the difficulty presented to us by other Hawaiian genera with stone-fruits, such as Elæocarpus, or with berries containing large seeds, such as Sideroxylon.

Sicyos (Cucurbitaceæ).—This genus comprises about thirty-five known species, of which three-fourths are confined to the New World, being mainly South American, whilst the remainder are restricted to Hawaii, with the exception of two species in the Galapagos Group and Norfolk Island, and a widely-ranging species, S. angulatus. The plant just named, the small fruits of which possess hooked spines, adapting them for dispersal in a bird's plumage, occurs in Africa, Australia, New Zealand, and America, but has only been recorded in the Pacific islands from the Kermadec Group.

North America was probably the home of the original Hawaiian species. Hillebrand describes eight species, of which five are not found in more than one island, whilst one species is spread over most of the islands. The fruits vary much in size, and only in a couple of species do they now possess any fitness for attaching themselves to plumage, some of them being pubescent or even glabrate, so that deterioration in the capacity for dispersal has here taken place. Their size is usually a quarter to half an inch (6—12 mm.); but it is noteworthy that the species with the largest fruit (Sicyos cucumerinus, one to two inches, or 25 to 50 mm.) is the species most widely dispersed over the group. This appears to indicate that there is some other means of inter-island dispersal in this archipelago than by attachment to birds' plumage. The isolation of the genus in Hawaii from the rest of the world is, however, complete, since all the species are endemic; and when, therefore, we come to ask how Sicyos angulatus, that has been dispersed in the recent era over America, Australia, and New Zealand, is not found in these islands, we are brought face to face with the ever-recurring difficulty, the suspension in later times of the agency of dispersal in the tropical North Pacific.

Jacquemontia (Convolvulaceæ).—This genus, which is chiefly American, is represented in Hawaii by a peculiar species, J. sandwicensis. This species grows occasionally on the sandy beaches associated with Heliotropium anomalum and Tribulus cistoides; but it is most at home on rocky ground and on old lava-flows near the sea-border, making its abode often in the pockets of black

sand produced by the disintegration of the lava. Its small seeds sink in sea-water even after prolonged drying; and it can perhaps be supposed that the original seeds were brought from North America in the crevices of a drifting log. According to Ridley, Fernando Noronha possesses a peculiar species also growing near the sea; and it may be that the drifting log has here been the agent also: but in neither case would this explanation account for the endemic character of the species.

Cuscuta (Convolvulaceæ).—It would seem that with the exception of Hawaii, where an endemic species, C. sandwichiana, occurs, no other oceanic group in the globe possesses a peculiar species of the Dodders. With the exception of an endemic species in New Zealand, and an introduced species in Fiji which is found usually near the gardens of the white residents on Viti Levu, the genus takes but little part in the Pacific floras. The Hawaiian species is a characteristic beach-plant growing on Ipomea pes capræ, Scævola Kœnigii, Tribulus cistoides, and on other plants that find a permanent or a temporary abode on the beaches. We learn from Ridley and Moseley that Cuscuta americana in Fernando Noronha finds its host also in Ipomea pes capræ. Since the seeds of the Hawaiian plant and of the introduced Fijian species possess no buoyancy, even after drying for years, we cannot look to the agency of the current unless we call the drifting log to our assistance, and in that case the endemic character of the Hawaiian species would present the difficulty already alluded to in the case of Jacquemontia. The seeds of the Hawaiian plant are about one-twelfth of an inch (2 mm.) in diameter, and as far as size is concerned they might have been transported in a bird's stomach; but, on account of the rapidity with which the seeds of the genus absorb moisture and swell up, it is most unlikely that they would escape injury. This is one of the several difficulties in plant-dispersal which New Zealand and Hawaii share in common. Further remarks on the germination of the Hawaiian species are made in Note 69.

Rumex (Polygonaceæ).—Hawaii possesses two peculiar species of Rumex, a genus not recorded from any other of the Polynesian groups. One of these species, R. giganteus, is a very remarkable plant, growing to a height of thirty or forty feet when supported by trees. It is noteworthy that the small group of Tristan da Cunha in the South Atlantic possesses a species, R. frutescens, confined to those islands (*Bot. Chall. Exped.*, ii. 154). Both Hawaii and Tristan da Cunha lie in mid-ocean, cut off from the nearest continent by some

1,800 or 2,000 miles of sea; and we may have to choose between the bird and the current in selecting the agency concerned with the transportation of the original seeds; or perhaps they have co-operated. Birds could disperse the nutlets of Rumex as readily as they do those of Polygonum, and I have found these fruits at times in the stomachs of partridges. On the other hand, Rumex fruits occur amongst the drift stranded on beaches in England and in Scandinavia; and, as indicated by the observations of Sernander and myself in these two localities, they float through the winter in ponds and rivers, germinating afloat in the spring. The nutlets sink, but they owe their buoyancy to the persistent perianth. In my sea-water experiments the fruits of Rumex hydrolapathum and R. conglomeratum were still afloat after from six to twelve months' immersion, and their seeds subsequently germinated. It is quite possible, therefore, that currents can carry these fruits unharmed to oceanic island-groups like Hawaii and Tristan da Cunha.

Dracæna (Liliaceæ).—This Old World genus, which on account of its berries is eminently suited for dispersal by frugivorous birds, is represented in Polynesia by a solitary species (D. aurea) peculiar to the Hawaiian Group. Attaining a height of twenty to twenty-five feet, it often forms a striking feature in the vegetation of the open wooded regions up to altitudes of 3,000 feet. I found it growing in abundance in the large island of Hawaii between Waimanu and Waipio, and on the northern slopes of Hualalai. It grows in a variety of stations, and I came upon it once in the broken-down caverns of an old lava-flow that were frequented by pigeons which no doubt brought the seeds. Its conspicuous yellow berries have hard rounded seeds a quarter of an inch (6 mm.) across and weighing two to three grains when dry, which would probably withstand injury in a bird's stomach, the minute embryo being protected by a very tough albumen. Neither the entire berry nor the seed could be transported by currents, the last sinking even after drying for six years.

Naias (Naiadaceæ).—If we except New Caledonia, where two or three species have been found, Hawaii is the only island-group in the tropical Pacific from which this interesting world-ranging genus of submerged aquatic plants has been recorded. Chamisso, the celebrated naturalist of Kotzebue's expedition, collected Naias marina in Oahu in the early part of last century; but apparently it did not come under Hillebrand's observation in the group. However, in 1897 I found it in another locality, namely, just within the mouth of the Waipio, a river on the north-west side of the

island of Hawaii. The mature fruits of this genus have never been experimented on by me; but there is nothing in the structure of the fruits to indicate that they have any buoyancy, or to show that they differ in this respect from the fruits of other completely submerged aquatic plants like Ceratophyllum, Ruppia, and some of the Potamogetons. It is to ducks and other waterfowl that we must attribute the dispersal of this and the other genera just mentioned over wide tracts of ocean, a subject dealt with in discussing those plants.

The Hawaiian Group probably represents the most isolated locality occupied by this genus, since none of the other islands from which species have been recorded, such as New Caledonia, Mauritius, and Bourbon, are so far removed from continental regions. The source of the Hawaiian form of Naias marina lies evidently on the Asiatic side of the Pacific, since it is referred by Mr. Rendle to the variety "angustifolia," an Asiatic plant found also in the island of Bourbon and in West Australia, but not recorded from the New World. The important little monograph of the genus by Mr. Rendle ("Naiadaceæ," in Engler's *Das Pflanzenreich*, 1901) is full of suggestiveness for the student of plant-distribution. His interest is excited when he discovers that one of the most typical genera of aquatic plants displays the same principle of differentiation at work that is so well illustrated by many of the land genera of the Pacific islands. I refer to the principle implied in the existence of a widely-ranging genus comprising "a polymorphic species occurring over almost the whole area of the genus," as well as a number of less widely distributed species, most of which have "restricted areas and fall for the most part into small geographical groups." I have just been quoting Mr. Rendle's description of the distribution of Naias, the "polymorphic" species concerned being N. marina; but it need scarcely be remarked that it would apply just as well to several of the land genera dealt with in the previous chapter (XXVI.), such as Alphitonia, Metrosideros, Pisonia, &c.

Although there is such a contrast in the degree of uniformity of their life-conditions between land and water plants, a strictly aquatic plant being but slightly affected by changes in the physical conditions that are accompanied by a complete transformation in the character of the terrestrial vegetation, yet—and this is the important point—we find the same principle of differentiation at work with both land and water plants. If one wished to produce proof of the contention that the production of new species is largely independent of external conditions, one could not do better than

take the cases of Elæocarpus, Metrosideros, and Naias. In all cases we see a widely-ranging polymorphous species settling down and "differentiating" in particular localities or regions, and forming subcentres for the distribution of the genus.

Potamogeton (Potameæ).—Though well suited for dispersal by waterfowl, the Potamogetons have been recorded from the Hawaiian and Marianne Islands alone among the tropical groups of the open Pacific. The genus, though not so well represented in insular floras as we might have expected, is still not infrequently to be found. Widely-ranging species have been observed in the Azores, Madeira, and the Canaries in the Atlantic, as well as in Hawaii in the Pacific; whilst species have been recorded that are peculiar to Martinique, the Mascarene Islands, and to the Marianne Group. Hillebrand gives for Hawaii, Potamogeton fluitans, a plant of the Old and New Worlds, and P. pauciflorus, a North American species; whilst in the *Index Kewensis* a peculiar species, P. owaihiensis of Chamisso (which is, however, regarded by Hillebrand as a form of P. fluitans), is also accredited to the group. Owing, however, to the paucity of streams and rivers this genus takes no prominent part in the Hawaiian flora, and the species seem to have been recorded alone from Oahu. As they were discovered by Chamisso in the early part of last century they are in all probability truly indigenous in Hawaii, even if none are peculiar to the group.

That ducks and similar birds are the agents in carrying the seeds of Potamogeton to oceanic islands cannot be doubted. About twelve years ago I examined the stomachs and intestines of thirteen wild ducks obtained in the London market. Three of them contained in all forty-one Potamogeton seeds, or rather "stones," most of which subsequently germinated in water. In one of my experiments, carried out in the month of December, I fed a domestic duck with the fruits of Potamogeton natans. They appeared in quantity in the droppings, for the most part divested of their soft coverings, but otherwise uninjured. Sixty per cent. germinated in the following spring; whilst of those left in the vessel, from which the duck had been fed, only one per cent. germinated in the next spring, and another year elapsed before any number did so. These results were published in *Science Gossip* for September, 1894.

One often reads in books of travel interesting remarks bearing indirectly on the dispersal of the Potamogetons. Thus, when Sir Joseph Hooker (then Dr. Hooker) noted in his *Himalayan*

Journals the occurrence of P. natans in the Neongong Lake in the Himalayas, and the presence of coots, he most probably mentioned the bird that brought the plants, coots being active distributors of the seeds of water plants. It is of importance to remember that (as shown in my experiment on the duck) seeds of water-plants are voided in a condition peculiarly favourable to early germination. Ducks, coots, and other water birds might often be characterised as "travelling germinators." My experiment showed that seven to eight hours at least were occupied by Potamogeton nutlets in passing through the digestive canal of a duck, and that probably nine or ten hours would be required after an average full meal. But this does not represent the possible maximum period, since the bared "stone" may remain in the gizzard for a long time with ordinary gravel. Most of the Potamogeton fruits found by me in wild ducks were obtained from the gizzard, where they were mixed with gravel and other hard seeds or seedvessels, as described in Chapter XXXIII. Such fruits afterwards germinated. With regard to the chances, therefore, of the fruits of Potamogeton being carried by a bird without injury across an ocean, we may infer that, whether they are retained in its body for only ten hours or for as long as three or four days, they will preserve in some cases their germinating power.

Hawaiian Genera found in Tahiti to the Exclusion of Fiji.

Taking only the genera that are strictly indigenous, and excluding therefore all those introduced by the aborigines, the number available for establishing an independent connection between the Hawaiian and Tahitian regions is exceedingly few. Amongst the Hawaiian shore-plants not found in Fiji proper but occurring in the Tahitian region are Heliotropium anomalum and Sesuvium portulacastrum. The last-named, however, has been recorded from Tonga, which lies within the Fijian area; whilst the first will probably be found in the same region. Amongst the Hawaiian and Tahitian mountain genera not recorded from Fiji proper are Nertera, Vaccinium, Cyathodes, and Luzula. As is pointed out in Chapter XXIII., the absence of these genera from Fiji is connected with the relatively low elevation of those islands, though it is quite possible that one or more of them may yet be found on the highest summits of Fiji; and indeed Nertera depressa

and Vaccinium have been discovered in the more elevated uplands of Savaii in Samoa.

After removing the littoral plants and the mountain genera, there are probably not more than half a dozen inland genera that connect the Hawaiian lowlands with the Tahitian region to the exclusion of the Fijian Group ; and Byronia (Ilicineæ), Reynoldsia or Trevesia (Araliaceæ), Phyllostegia (Labiatæ), and Pseudomorus (Urticaceæ) may be taken as examples. Of these, Pseudomorus, which has a small drupaceous fruit suitable for dispersal by frugivorous birds, has been recorded from New Caledonia, and not improbably it exists in the Fijian area ; and the same may be postulated of Reynoldsia, which is discussed in a later page, since it has been found in Samoa. We may almost form the same opinion of Byronia, since it exists in Australia. This genus of small trees contains only three known species, one in Australia, one in Tahiti, and one in Hawaii. Its fleshy drupes, about a third of an inch (8 mm.) in size, would attract birds, and their numerous cartilaginous pyrenes would probably pass unharmed through a bird's alimentary canal. Phyllostegia, a Labiate genus with fleshy nucules that might attract birds, is, with the exception of a solitary Tahitian species, entirely confined to Hawaii (see Chapter XXII.).

From these data it may be inferred that the interchange of plants between the regions of Hawaii and Tahiti to the exclusion of Fiji has been very slight. The facts of distribution are just such as we might look for in the case of a general dispersal over the oceanic groups of the tropical Pacific, with the altitudes of the islands playing a determining part. In this general dispersal Hawaii has shared ; and except in the case of Phyllostegia it is evident that this group has kept nearly all it received and has distributed but little.

Hawaiian Genera found in Fiji to the Exclusion of Tahiti.

We shall be able to throw further light on the floral history of Hawaii by discussing the few tropical genera, not a score in all, that it possesses in common with Fiji to the exclusion of the Tahitian region. The following genera offer themselves for treatment :—Eurya (Ternstrœmiaceæ), Gouania (Rhamnaceæ), Maba (Ebenaceæ), Sideroxylon (Sapotaceæ), Antidesma (Euphorbiaceæ), Pleiosmilax (Smilaceæ), and Ruppia (Potameæ).

These seven genera, which with the exception of Ruppia, an aquatic genus, are only represented in Hawaii by peculiar species, possess in all cases, except Gouania and the last-named genus, drupaceous or baccate fruits likely to attract frugivorous birds. Two of them, Eurya and Antidesma, have their home in Malaya and in the Asiatic continent; three of them, Gouania, Maba, and Sideroxylon, are found on both the Asiatic and the American sides of the Pacific Ocean; whilst Pleiosmilax should, strictly speaking, be regarded as a Polynesian subgenus of Smilax, a world-ranging genus; and Ruppia is a cosmopolitan brackish- and salt-water genus.

It is highly probable that Fiji received almost all these genera from the Old World through Malaya; and in some cases the resemblance between the Malayan and the Fijian species is so close that, as in Gouania, Dr. Seemann questioned if they were not forms of the same species. In other instances, as with Maba, we find a widely-ranging Asiatic and Malayan species, like Maba buxifolia, extending into Western Polynesia, where it is accompanied by other species peculiar to that region. But if the genera were able subsequently to extend their range thence to Hawaii, it is difficult to understand why they have not reached the Tahitian region. It is therefore likely that Hawaii received most of these genera by a northern route and not through the South Pacific; and it is legitimate to suppose that when Old World genera like Eurya and Antidesma occur in north-eastern Asia, as in Japan and in the neighbouring mainland, Hawaii received the genus by that route. In the case of Eurya it is noteworthy that Fijian and Samoan forms, regarded by Seemann and Gray as distinct species, are viewed by Reinecke as forms of E. japonica, an extremely variable species found in Japan. With genera like Gouania and Maba, that exist on both sides of the Pacific, it is possible that they may have originally reached Hawaii from America.

A noticeable feature in the instance of genera like Maba and Sideroxylon is that hard seeds or pyrenes $\frac{3}{4}$ to 1 inch (18 to 25 mm.) in length have seemingly been transported by frugivorous birds across the ocean to Hawaii. This at first sight seems improbable; but it is known that fruit-pigeons can swallow very large drupes, as in the case of those of Canarium, Dracontomelon, and Elæocarpus, afterwards disgorging the "stones." They have carried such stones to Fiji, across some 500 or 600 miles of ocean; and unless we impute a continental origin to Hawaii we must assume that in some cases, as with Elæocarpus, Maba, and Sideroxylon, they have been able to

transport these large stones or pyrenes to that group. The extent of ocean to be crossed is no doubt much greater, but this area of the Pacific is not without some small half-way groups that would serve as resting-places.

That fruits of the order Sapotaceæ are much appreciated by fruit-pigeons is already known. We learn from Kirk that the fruits of Sideroxylon costatum (Sapota costata) are a favourite food of the New Zealand fruit-pigeon, the fruits, about an inch long, containing three hard crescentic bony seeds nearly as long as the fruit. The natives of Vanua Levu informed me that a Fijian species of Sideroxylon with hard seeds about an inch long was much appreciated on account of its fruit by the pigeons. I found the hard, sound seeds of a species of Sapota, two-thirds of an inch (or 16 mm.) in size, in the crop of a Fijian fruit-pigeon. The similarly large seeds of a species of Achras were identified by Mr. Charles Moore, of Sydney, amongst a collection of seeds, &c., found by me in the crops of fruit-pigeons shot in the Solomon Islands (Guppy's *Solomon Islands*, p. 293). It may be added that the difficulty concerned with Sideroxylon in Hawaii is the difficulty concerned with other large-seeded Sapotaceous trees in Fiji and New Zealand, and the same explanation must be applied to all. Some further remarks on the Sapotaceæ in the Pacific are given below.

The mode of dispersal of some of these genera is illustrated in other regions. The berries of Pleiosmilax, a subgenus of Smilax, are well suited for aiding the dispersal of the genus by frugivorous birds ; and we learn from Prof. Barrows (Weed, p. 42) that in the United States crows feed on the fruits of Smilax rotundifolia and disperse the seeds. On the other hand, it is not at first sight easy to understand how a genus like Gouania has been distributed over the tropics of the globe, since it possesses dry capsular fruits about half an inch across, separating into three woody cocci that appear most unlikely to attract birds. The same difficulty exists, however, with other dry-fruited widely-ranging genera like Alphitonia and with many of the Euphorbiaceæ.

Amongst these genera found in Hawaii and Fiji to the exclusion of Tahiti we can at times detect indications of the operations of a polymorphous species as described in Chapter XXVI., when a widely-ranging highly variable species is associated in some groups with peculiar species. We see some evidence of this in the genera Gouania, Maba, and Eurya, alluded to on a previous page. (See also *Bot. Chall. Exped.*, iii. 134, under "Gouania.")

One of the mysteries of the Pacific is concerned with the distribution of the Sapotaceæ, the dispersal of which by frugivorous birds has been dealt with above. It is strange that whilst the order seems to have found a *rendezvous* in Tonga, no one except Horne appears to have recorded any of the genera from Samoa. They are fairly well represented in Fiji; but it is in Tonga that we especially note the gathering together of several Sapotaceous trees with large heavy seeds, of the genera Bassia, Mimusops, and Sideroxylon. Besides owning one or two species of Sideroxylon in common with Fiji (Burkill), this small group possesses Bassia amicorum and Mimusops kauki, both of which were found there by Forster at the time of Cook's visit. In a list of a small collection of plants made by him in Upolu in the Samoan Group about 1879, Horne includes two species of Sideroxylon (*Year in Fiji*, p. 286); and according to Seemann there is a Sapotaceous tree in Wallis Island. A species of Bassia exists in Rarotonga, the seeds of which, from Mr. Cheeseman's description of the fruit, must be almost an inch long. Drake del Castillo refers to an endemic Tahitian tree near Mimusops; but its fruit was not known to him.

As already indicated, the difficulties connected with the Sapotaceæ affect the whole Pacific from New Zealand north to Hawaii and from Fiji east to Tahiti. We are driven to appeal to the agency of frugivorous birds, at least in the case of Sideroxylon, since some fruits experimented on by me in Fiji sank at once or in a day or two, the seeds having no buoyancy. That birds actually disperse the seeds of this and other genera of the order has been already pointed out, yet it is possible that currents have at times aided in the dispersal of some of the genera. This is indicated by the circumstance that, as we learn from Schimper, some Sapotaceous trees are to be included in the Malayan strand-flora, namely, Sideroxylon ferrugineum, Mimusops kauki, and M. littoralis, all occurring as well on the Asiatic mainland, the first growing also in the Liukiu Islands, and the last in the Andaman and Nicobar Groups.

Ruppia maritima (Potameæ).—This cosmopolitan aquatic plant has only been recorded in Polynesia from Hawaii, Samoa, and Fiji. It had not been collected in Fiji before my discovery of it in 1897. Amongst other oceanic islands where it occurs may be mentioned the Bermudas, where, according to Hemsley, it exists as an indigenous plant in the lagoons. Chamisso first noticed it in Hawaii, and Hillebrand remarks that

it grows in shallow waters along the coasts. Amongst other localities where I noticed it in this group may be mentioned the north-west coast of the large island of Hawaii between Kailua and Keahole Point. Here in 1896 it was thriving in brackish-water ponds, with Sesuvium portulacastrum growing at the edges. Reinecke observes that it occurs in similar ponds in Samoa. In 1897 I found it in abundance in the Rewa estuary (Fiji), both in the creeks and in the main channel. In the following year it was not to be found in this locality, a circumstance noticed both by the natives and by resident whites. The fruits of this plant possess no floating power, sinking, even after prolonged drying, in a few hours. It is to ducks and to birds of similar habit that its dispersal must be attributed.

The Absentees from Hawaii.

It has been before remarked that of the 330 or 340 genera of flowering-plants recorded from Fiji some 200 are not known in Hawaii. It will only be possible to deal with the absent genera in a cursory manner; but enough will be done to show that we are face to face here with a multitude of the seeming inconsistencies that so often beset the study of plant-distribution.

A host of plants are unrepresented in Hawaii, of which it may be said that their seeds or fruits are not less suited for being carried across the Pacific than those of many that are now in that group. On the other hand, a number of genera exist there which we should never expect to have been endowed with the capacity, and to have received the opportunity, of crossing nearly 2,000 miles of ocean. Yet perhaps when Nature acts in a wholesale fashion and excludes entire orders we may be able to perceive the dim outlines of a principle of exclusion at work. But even here much caution and some clearing of the ground are needed.

For example, having regard to the several modes of dispersal possessed by the great variety of fruits and seeds of the Sterculiaceæ, it would be almost meaningless to remark that the order so well represented in Fiji is practically non-existent in Hawaii as far as truly indigenous plants are concerned. It is true that two species of Waltheria are here present, but one of them W. americana, is a weed probably introduced by the aborigines whilst the other, W. pyrolæfolia, recorded from a solitary locality by the Wilkes Expedition, has seemingly never been found since. From the standpoint of dispersal the genera Sterculia, Heritiera,

Kleinhovia, Melochia, and Commersonia, that are represented in Fiji but not in Hawaii, cannot be discussed together. With Sterculia is concerned the dispersal by birds of large seeds, an inch in length, not particularly well protected, the genus being confined to Fiji alone of all the oceanic Pacific groups. Heritiera is only represented by a littoral species, the large fruits of which are carried great distances by the currents; and no other agency of dispersal is here possible. The last three genera are distributed over the South Pacific, their relatively small seeds being probably in the main dispersed by granivorous birds; whilst the setose fruits of Commersonia may have been at times transported in birds' plumage.

It is more legitimate, perhaps, to speak collectively of the orders Meliaceæ and Melastomaceæ as absent from Hawaii; but even here the issue raised is one concerned rather with opportunities than with capacities for dispersal. Several years ago, M. Casimir de Candolle remarked that "it is hardly credible that the Meliaceæ should be entirely absent from the Sandwich archipelago" (*Trans. Linn. Soc. Bot.*, vol. i. 1880). Yet it can scarcely be said that this is a matter connected with means of dispersal. Amongst the Meliaceous genera represented in Fiji, Vavæa and Aglaia have a berry, Melia has a drupe, and Dysoxylum has a capsule. So again with the Melastomaceæ; it possesses at least six genera in Fiji, two in Tahiti, and none in Hawaii. Whilst the genera Melastoma and Medinilla have baccate fruits with minute seeds, Astronia has a capsule with similar seeds, and Memecylon has a single-seeded berry. Since, however, minute seeds are most typical of the order, those of Melastoma denticulatum being about one-fiftieth of an inch or ·5 mm. in size, it would seem that this character has not aided its dispersal in the Pacific so far as Hawaii is concerned. From the circumstance that berries, drupes, and capsules are represented in these two Fijian orders we may form the opinion that their non-occurrence in Hawaii is due not so much to lack of capacities for dispersal as to failure of opportunities.

This opinion is much strengthened when we come to deal with the individual genera, where the predominant cause of the absence of so many Fijian genera from Hawaii is concerned with the failure of the agencies of dispersal. It is not a question of a difference in size between the groups, since, although the surface-area is approximately the same in both groups, Hawaii possesses only two-thirds of the number of genera occurring in Fiji. It is not

a question of capacity for dispersal across an ocean, since birds have transported across the Pacific to Hawaii the "stones" and large seeds of genera like Elæocarpus and Sideroxylon, a feat that would have been deemed impossible by many botanists. It is no lack of capacity for dispersal that has excluded Loranthus from Hawaii and has admitted Viscum.

Few genera, indeed, would seem to be better fitted for dispersal by frugivorous birds in the Pacific than that of Ficus. Its fruits are known to be eaten by birds all over the area of the genus; and we find the species distributed over the South Pacific from Fiji to Tahiti, but they are quite absent from Hawaii. This is the more remarkable on account of the occurrence of a species of Ficus resembling a banyan in Fanning Island about 900 miles south of the group (*Bot. Chall. Exped.*, iii. 116, 194), and because the Hawaiian Islands possess the Meliphagidæ or Honey-eaters, which are widely distributed in Polynesia and are known to feed on these fruits—a matter further discussed in my treatment of Ficus later on in this chapter.

Of several Rubiaceous genera with fleshy fruits that are represented both in Fiji and Tahiti, such as Stylocoryne and others, and of those Rubiaceous genera with minute seeds that, like Ophiorrhiza, are distributed over the South Pacific, none occur in Hawaii. Here we find represented other genera of the order, like Gardenia, Plectronia, and Coprosma, that do not appear to be better fitted for dispersal by frugivorous birds than many of the genera not existing there. If birds have carried to Hawaii in their plumage the fruits of Pisonia and Sicyos, it cannot be merely a question of capacity for dispersal that is concerned with the restriction to the South Pacific of genera with hairy seeds, such as Trichospermum, Alstonia, and Hoya.

It is unnecessary to dwell longer here on the subject of the Hawaiian absentee-genera, since many of the absent plants will be discussed when dealing with the peculiarities of the Fijian flora. The data there given all go to show that mere lack of capacity for dispersal over the Pacific often counts for little in supplying us with an explanation of the absence of so many likely genera from the Hawaiian flora. Hawaii has only been stocked with those genera common to Fiji and Tahiti that could have reached it during each age of general dispersal over the Pacific. In later eras the dispersing agencies have been mainly active in the tropical South Pacific; and thus it is that, as will be pointed out in a later page, the bulk of the plants of the Malayan era are confined to the region between

Fiji and Tahiti. In a still later period the dispersing agencies have confined their operations mainly to Western Polynesia and the last immigrant genera have not reached beyond the Fijian region.

The whole story of plant-life in the tropical Pacific is bound up with these successive stages of decreasing activity of the dispersing agencies. The story of plant-distribution in this region is well illustrated in its earlier phases of general dispersion in the floral history of Hawaii, in its later phase by those Asiatic genera that have only crossed the South Pacific to Tahiti, and in its last phase by those genera that have never extended beyond the groups of the Fijian area. The area of active dispersion, that first comprised the whole of the tropical Pacific, was afterwards restricted to the South Pacific, and finally to the western portion of that area. It can scarcely be doubted that these successive stages in the contraction of the area of active dispersion of plants in the Pacific were accompanied by a corresponding diminution in the general distribution of birds in the same ocean, to which it stood in the relation of an effect to a cause.

Tahiti.

The peculiarities of the Tahitian flora as compared with Hawaii and Fiji may be discussed by treating first those genera that are alone represented in Tahiti, the " residual " genera ; then those that it possesses in common first with Hawaii and then with Fiji ; and lastly by pointing out the more noticeable gaps in the flora. By Tahiti is typically signified the whole Tahitian region, which includes the Austral and Cook Groups, the Society Islands, the Paumotus, and the Marquesas.

The Tahitian Residual Genera.

The non-endemic genera occurring alone in the Tahitian region and not found either in Hawaii or in one or other of the three groups of the Fijian region (Fiji, Tonga, Samoa) are not more than half a dozen. These six genera are exceedingly interesting ; but since each tells a different story and gives its own independent indication they cannot be treated in a collective sense. Nor are they all to be regarded as anomalies in plant-distribution, since with a single exception there is scarcely one concerning which it is not in some way possible to give an explanation of its isolation without coming into conflict with the principles of plant-dispersal. The exception is Lepinia tahitensis, which, without presenting any

very evident capacity for dispersal, has not been recorded from any other localities in the Pacific than the far-separated Solomon and Tahitian Groups. There is a suspicion that, as in the case of the residual genera of Hawaii, America may have contributed some of the original plants, since three of the genera, Buttneria, Coriaria, and Bidens, occur in that continent, and in the case of Coriaria Tahiti possesses a species found in South America as well as in New Zealand.

One of the trees in question is Cratæva religiosa, an Asiatic species, which may be placed among a group of trees, including Cananga odorata and Fagræa Berteriana, which, whilst they are much esteemed by the inhabitants of the South Pacific for their fruits or their flowers, and are often planted in and around their villages, possess fruits that attract birds, and in the case of Cananga are known to be dispersed by fruit-pigeons. Probably the aborigines and the birds have worked together in the distribution of these trees.

The genera Buttneria of the Sterculiaceæ and Berrya of the Tiliaceæ are represented in this region by species that must owe their dispersal to birds, though I have no data relating to the matter of their dispersal, their fruits being capsular, in the first case prickly. Coriaria is a mountain genus in Tahiti and will be found discussed in Chapter XXIV. in connection with the Tahitian mountain-flora. Its absence from the West Polynesian groups is no doubt to be connected with their insufficient altitude. In addition to the introduced Bidens pilosa, a common tropical weed, Tahiti possesses two other truly indigenous species of Bidens, of which one at least is peculiar to the region. The achenes of this genus are well known to be adapted for dispersal in a bird's feathers ; and since the genus has its principal home in America, no other indigenous species having been recorded from South Polynesia, it is not unlikely that the parent species was American.

One of the numerous enigmas of the Pacific floras is concerned with the presence in the islands of Tahiti and Moorea (Eimeo), in the Society Group, of the Apocynaceous tree, Lepinia tahitensis. The genus contains this solitary species, which has been collected only in one other locality, namely, in the Solomon Group, where it was obtained by the Rev. R. B. Comins. Such an instance of disconnected distribution is rare in the Pacific Islands, and undoubtedly it represents one of the difficulties of the Tahitian flora. The fruits, which are indehiscent and five or six inches in length, possess a fibrous pericarp and a single seed.

No data are to hand relating to the capacities for dispersal possessed by this plant, but it is certain that it has had some means of crossing the sea between the adjacent islands of Tahiti and Moorea. (See Hemsley, *Journ. Linn. Soc. Bot.*, xxx. 165.)

Tahitian Genera found in Hawaii to the Exclusion of Fiji.

This subject has been already discussed in this chapter in dealing with the genera restricted to Hawaii and Tahiti.

Tahitian Genera found in Fiji to the Exclusion of Hawaii.

Excluding the orchids, sedges, and grasses, as well as the few endemic genera, between sixty and seventy genera, or rather less than half of the genera of the flowering-plants of Tahiti, are found in Fiji to the exclusion of Hawaii. Of these, rather over a half are Old World genera ; about a third occur in both the Old and the New World ; four are confined to Polynesia, and not one is exclusively American. One-third are genera now possessing in the Tahitian region endemic species either entirely or in part, and in such cases we may consider that the agencies of dispersal are now inactive or partially suspended ; the others belong entirely to the present era of dispersal. About half have more or less fleshy fruits fitted for dispersal by frugivorous birds. About a fourth have capsular or other dry fruits that must have been also dispersed by birds preferring a drier diet. Three only possess hairy seeds or fruits suitable for being carried in a bird's plumage, namely, Commersonia, Weinmannia, and Alstonia. There remain about a fourth of the total that are shore-plants dispersed by the currents, being in two cases (Ximenia and Kleinhovia) assisted by birds; whilst Triumfetta, another littoral genus, is probably distributed by birds alone.

There are no cases of special difficulty from the standpoint of dispersal in these sixty and odd non-endemic genera that Tahiti possesses in common with Fiji to the exclusion of Hawaii. The lack of difficulties connected with the dispersal of all these Tahitian genera is worthy of note, because there are very few difficult genera amongst the rest of the Tahitian flora. Excluding Lepinia tahitensis, which has been already referred to, there are scarcely any "impossible" plants in the Tahitian region ; and even in this case, when the modes of dispersal of Lepinia come to be

investigated, it is likely that much of the difficulty will disappear. Hawaii, as we have before seen, abounds with perplexing questions of this nature. When dealing with the absentee Tahitian genera, later on in this chapter, it will be shown that "size" has played a prominent determining part in the exclusion of genera from Tahiti, genera with seeds or "stones" exceeding half an inch or twelve millimetres in dimension being, as a rule, unrepresented amongst the truly indigenous plants.

My further remarks on these Tahitian genera found in Fiji but not in Hawaii will be limited to some general observations from the standpoint of dispersal. I will first discuss some of those genera that possess only peculiar species. They belong to an era of dispersal that, as far as Tahiti is concerned, is passing or has passed away. Here we have the species of each genus more or less localised in the various South Pacific archipelagoes; but, as with Meryta, Alstonia, and Loranthus, it is often apparent that, although the Tahitian region is mainly outside the zone of present dispersal, the different groups of the Western Pacific are kept in touch by the possession of species in common. This testifies to the activity of dispersal in that region after it had become suspended in Eastern Polynesia. The connection between the isolated endemic species of Eastern Polynesia and a species ranging over the Western Pacific can sometimes be shown, as in the case of Loranthus, where a species confined to the Society Islands and to the Marquesas is very closely related to L. insularum, a widely-ranging West Polynesian species that reaches eastward as far as Rarotonga.

We next have those genera like Grewia, Nelitris, Melastoma, Randia, Geniostoma, Tabernæmontana, Fagræa, Bischoffia, Macaranga, and Ficus, that possess in Polynesia one or more widely-ranging species. The agency of the polymorphous species, which I have described in the preceding chapter in connection with the general dispersal of Malayan plants over the whole of Polynesia, is evidently also active when the work of dispersal is restricted to the South Pacific. Its operation is to be distinctly traced in all the genera above named except in Fagræa and Ficus. Thus, in the genera Grewia, Melastoma, Randia, Geniostoma, and Macaranga we find a single variable species ranging over the South Pacific from Fiji to Tahiti, keeping all the groups in touch, but associated in each, as a rule, with one or more peculiar species. A yet earlier stage in the process is to be seen in those genera which, like Nelitris, Tabernæmontana, and Bischoffia, possess only a solitary

species ranging over the South Pacific, varying in each group, but not usually associated with endemic species. As with Melastoma, Macaranga, and others, we can often trace the widely-ranging species of Polynesia back to its home in Malaya, and with these and other genera the connection between a species confined to a group and a variable species ranging through all the archipelagoes of the South Pacific can sometimes be detected in the affinity of their characters.

It is thus seen that one of the principal determining causes of the differentiation of species in Polynesia lies in the failure of the dispersing agencies, a widely-ranging species becoming in consequence gradually isolated in the various groups. With some genera, as with Ophiorrhiza, it is possible to show that the resulting endemic species pass into each other by intermediate forms.

My further remarks on the Tahitian genera occurring in Fiji but not in Hawaii will be devoted mainly to those with which I was most familiar from the standpoint of dispersal.

The Tiliaceous genus GREWIA offers a good example of those Polynesian genera which possess in the South Pacific a single widely-ranging species associated often with endemic species in the individual groups. It is likely that a polymorphous form, including most of the Polynesian species, could be here constituted. The fruits are dryish drupes, becoming black and moist when over-ripe, and containing three or four pyrenes suitable for distribution by birds and five or six millimetres in size.

The berries of NELITRIS, a genus of the Myrtaceæ, contain a few hard seeds that are well fitted for dispersal by frugivorous birds. I am inclined to follow Drake del Castillo, who considers that there is only one varying species, N. vitiensis (Gray), which is distributed over the whole of the South Pacific from the Solomon Islands to Tahiti. The tendency of this widely-ranging species to vary in different groups is indicated in the fact that some botanists have distinguished other species within these limits. It is noteworthy that N. paniculata in Indo-Malaya and N. vitiensis in the Pacific cover the whole range of the genus. It would be interesting to establish a connection between them.

MELASTOMA, an Old World genus of forty and more species, has one very variable species, M. denticulatum, which, as defined by Bentham, has the range of the genus from tropical Asia across the Pacific to Tahiti. This plant is associated in some groups, as in Fiji, Tonga, and Samoa, with other more or less localised species, and it affords a good example of the principle of polymorphism in

species-making. The berry-like fruits contain an abundance of minute seeds, half a millimetre in size, which, when rendered adhesive by adherent pulp, might readily stick to feathers, or they might pass unharmed through the alimentary canal of a bird. It is noteworthy that amongst the plants regarded by Prof. Penzig as introduced by frugivorous birds into Krakatoa since the eruption is a species of Melastoma.

Few genera in these islands would better repay a careful study of their species with regard both to the influence of station on specific characters and to the question of "mutations" than OPHIORRHIZA. I found the three Fijian species of this Rubiaceous genus so often in close association, that I cannot doubt there is some connection between them. Seemann and Gray, indeed, characterise two of them as confluent species. The island of Tahiti alone possesses five peculiar species, and it is evident that this island has been a centre of development for species of Ophiorrhiza, just as Samoa has become the birthplace of many species of the Urticaceous genus Elatostema. The minute angular seeds of Ophiorrhiza would probably be transported in a bird's feathers or in adherent soil. As my experiments showed, they do not become adhesive when wet.

The genus LORANTHUS as distributed in the South Pacific has already been briefly noticed. There is a species confined to the Tahitian region, and there is another peculiar to Samoa, whilst one widely-ranging species, L. insularum, that connects these regions together, reaching east to Rarotonga, is closely related with the Tahitian species. There was no doubt originally a single polymorphous plant that ranged over the tropical South Pacific. With regard to the mode of dispersal of the seeds of this genus of parasites, I should at once refer to the systematic and careful observations made by Mr. F. W. Keeble in Ceylon (*Trans. Linn. Soc.*, v. 1895–1901). He formed the opinion that the seeds of Loranthus usually reach their host without passing through the alimentary canal of a bird, being merely wiped off its bill. This method would never carry the seeds to Tahiti or even to Fiji; and since this observer remarks that, although most of the seeds in the droppings were completely rotten, some of them "possibly pass through the gut uninjured," we may accept this possibility as sufficient for the purpose of dispersal in the Pacific Ocean. Mr. Keeble notes the observation in Teil 3 of Engler's *Die Natürlichen Pflanzenfamilien* that the seeds may germinate after passing through a bird's intestine; and we may therefore infer

that whilst the method he describes is typical of local dispersal, the other method is required in the instance of oceanic dispersal.

ALSTONIA, an Apocynaceous genus of tropical Asia and Australia, yields the caoutchouc of Fiji. Besides possessing in Fiji and Samoa peculiar species, the islands of Western Polynesia have in A. plumosa a species common to Fiji, Samoa, and New Caledonia. Another species, A. costata, is restricted to Eastern Polynesia, occurring in the different islands of the Tahitian Group as well as in Rarotonga. It is possible that the Pacific species may be connected with A. scholaris, a species possessing the range of the genus with the exception of Polynesia. The long ciliated or hairy seeds, six to nine millimetres in length, are fitted for transport by the winds and in birds' plumage. The follicles dehisce on the tree, and, according to Horne, the light seeds are distributed locally by the wind. It is probable that the thick white juice oozing from a broken branch would at times aid the adhesion of the seeds to a bird's feathers.

GENIOSTOMA, a genus of the Loganiaceæ, is found in Malaya, Australia, and New Zealand. It possesses in G. rupestre a species that ranges across the South Pacific from New Caledonia to Tahiti, being associated with one or more endemic species in most of the groups. The fruit is a dehiscent capsule containing numerous small seeds imbedded in a yellowish pulp; and from the standpoint of dispersal it may be placed in the same category with Pittosporum and Gardenia (see pages 310, 313).

The same principle involved in the occurrence of a species ranging the South Pacific from New Caledonia to Tahiti, and associated with one or more endemic species in most of the principal groups, is illustrated in the Euphorbiaceous genus MACARANGA. It is specially noteworthy that M. tanarius, which ranges from India to East Australia and the New Hebrides, comes in touch in the group just named with M. harveyana, the widely-ranging plant of the South Pacific above alluded to, and itself an Asiatic species (see Burkill; *Bot. Chall. Exped.*, iii. 191; *Index Kewensis*). The connection between M. harveyana, the widely-ranging species of the South Pacific, and the endemic species in the various groups is indicated by its affinity with M. reineckei, a Samoan species. The Macarangas in Fiji grow in a variety of situations, on the borders of estuaries, in the mountain forests, and on the isolated mountain peaks. It is to birds that we must look for the dispersal of the genus. In the case of a species, apparently M. seemanni, common in the Rewa delta, the seeds, which soon fall

out of the cocci, are not infrequently found in the drift of the estuary, but they sink in a week or two. Other species examined showed no capacity for dispersal by currents. The fruit of M. harveyana is provided with a few prickles, but since it breaks up into the cocci, from which the seeds soon fall out, these appendages could scarcely aid its dispersal.

Like many other genera, TABERNÆMONTANA, an Apocynaceous genus distributed through the tropics, is represented in Polynesia by a widely-ranging species, T. orientalis, which extends from Malaya and Eastern Australia through all the large groups of the South Pacific from the New Hebrides to Tahiti, and is associated in Fiji with one or two peculiar species, one of which, according to Mr. Burkill, is nearly related to it. This genus therefore seems to illustrate the earliest stage in the Pacific of that process by which a widely-ranging species takes on a polymorphous habit and through its variations gives rise to different species in various groups. Prof. Schimper ranks T. orientalis amongst the Malayan strand-flora; but in Fiji the Tabernæmontanas are only littoral where the soil is rich as in alluvial regions; and they have no capacity for dispersal by currents that is worth speaking of, the seeds in the case of T. orientalis and another species sinking after drying for years, whilst the follicles soon open in water and go to the bottom in a few days. The observations of Gaudichaud and Moseley indicate that some Malayan species are dispersed locally by the currents (*Bot. Chall. Exped.*, iii, 279, 293); but the fruits of the genus are evidently quite unfit for oceanic dispersal by this agency. We find in the bird the agent that has carried the genus to the distant island-groups of the Pacific; and from the standpoint of dispersal the fruits may be placed with those of Pittosporum and Gardenia, being follicular, and in the Fijian plants possessing seeds, 5 to 10 millimetres in size, embedded in a pulp.

FAGRÆA, an Asiatic and Malayan genus of the Loganiaceæ, is represented in the Pacific by F. berteriana ranging through all the groups and islands of the South Pacific from the Solomon Islands and New Caledonia to Tahiti and the Marquesas, and by one or two other species in Fiji. It is with Fagræa berteriana that we are entirely concerned. The tree is often planted by the Pacific islanders near their villages; and since they value its timber and use its large fragrant flowers for personal decoration and for other purposes, it is probable that they have aided in its dispersal. But, as shown below, it behaves in most localities as an indigenous

plant; and its berries are well fitted for promoting its dispersal by frugivorous birds.

I was familiar with Fagræa berteriana both in the Solomon Islands and in Fiji; and in the last-named locality I especially studied it from the standpoint of dispersal. All over the South Pacific, whether in the Solomon Islands, in Fiji, in Rarotonga, or in Tahiti, this tree, though thriving also in the lower levels, especially frequents rocky scantily vegetated or open-wooded hill-tops and crests up to 2,000 or 2,500 feet above the sea. In the rich alluvial soil of the Rewa delta in Fiji it attains a height of 25 or 30 feet or more, whilst in the poor, dry soil of the "talasinga" plains in this group it is much dwarfed, and often does not exceed 10 feet, and may be only 6 feet high. It is in these "talasinga," or "sunburnt," plains of Fiji, especially in the Mbua province of Vanua Levu, that the tree, although dwarfed, seems most at home. Here it flowers and fruits abundantly whilst associated with Acacia, Casuarina, and Pandanus trees, and it is in such dry localities that this tree reflects in its choice of station the behaviour of different species of the genus in the Malay Peninsula, where they grow in open heath-country and sometimes on sandy heaths (Ridley in *Trans. Linn. Soc. Bot.*, iii, 1888-94). The fruits and seeds of F. berteriana have little or no capacity for dispersal by currents. On the Fijian plains the berries partially wither and rot on the tree. In the western part of its area this tree almost comes in touch with the Asiatic species, F. obovata, that ranges from India and Ceylon to the Malayan region, a species that must be indebted to frugivorous birds for its wide distribution.

The Euphorbiaceous genus BISCHOFFIA seems to offer another example of polymorphism in a wide-ranging species. Following Drake del Castillo, I take the genus as including only a single species, B. Javanica, a tree distributed over tropical Asia, Malaya, and Polynesia as far east as Tahiti. The variable character of the species is indicated by the different views held by the several botanists who have discussed the South Pacific species. Whilst it is a common forest-tree in Indo-Malaya, it affects in the Pacific islands the open-wooded districts of the lower levels, and it is not uncommon on the dry "talasinga" plains of Fiji. The fruits and seeds displayed in my experiments little or no capacity for dispersal by currents; nor do these dryish berries, with seeds four or five millimetres long, seem to be especially attractive for fruit-eating birds; and it is likely that the same birds that distribute Macaranga seeds also disperse those of this genus. The tree bears the same

name over the South Pacific, "koka" in Fiji and Rarotonga, and "oa" in Samoa. Like many other Polynesian trees, it has its uses, but there is no reason to believe that the natives have aided materially in its dispersal.

FICUS, a large genus comprising several hundred species, attains its greatest development in tropical Asia and in Malaya. It is well represented in the Western Pacific from the Solomon Islands to Fiji and Samoa; but in Eastern Polynesia the species are very few, and the genus is altogether absent from Hawaii, although a species has been found in the North Pacific in Fanning Island, about 900 miles south of the Hawaiian group (see page 377).

The Polynesian species are for the most part restricted to the Pacific islands, but there are only two species that range over the South Pacific as far east as Tahiti, namely, Ficus prolixa, the Tahitian banyan, and F. tinctoria. Some species are confined to Western Polynesia, such as F. obliqua, the Fijian banyan, F. scabra, and F. aspera, the last occurring in East Australia. Among the individual groups Fiji possesses probably fourteen or fifteen species, of which, perhaps, a third would be peculiar. According to Dr. Warburg, as cited in Dr. Reinecke's paper, Samoa owns eight species, of which six may be endemic. In Rarotonga and Tahiti we find only F. prolixa and F. tinctoria. The species in the groups where they are best represented belong to three or four sections of the genus.

The banyans of the South Pacific are represented by three or four species, namely, Ficus prolixa, the Tahitian banyan, found all over the tropical groups of the South Pacific from the New Hebrides and New Caledonia to Tahiti, the Marquesas and Pitcairn Island (Maiden); F. obliqua, the Fijian banyan, confined to the islands of the Western Pacific from the New Hebrides to Tonga; and two new banyans in Samoa, as described by Dr. Warburg in Dr. Reinecke's paper. In my paper on Polynesian plant-names it is shown that the banyans possess two names in the Pacific, one being "aoa," the Polynesian name, found in all the groups from Samoa eastward, and connected linguistically with the Malayan and Malagasy banyan-words; the other, the Melanesian name typified in the Fijian "mbaka," and represented in a variety of forms in the New Hebrides and neighbouring groups.

It is probable that the Pacific islanders have assisted in the dispersal of one or two of the species of Ficus, such as F. tinctoria, which they employ for different purposes, but, generally speaking, birds are active agents in distributing the genus. I need scarcely

say that the agency of the currents is quite insufficient to explain the distribution of Ficus. When in Fiji I experimented on three or four different species of Ficus belonging to the sections of the genus there represented. The fruits may float at first, but within a week or ten days they break down, and the seeds escape and sink. Beneath a tree of F. scabra growing on the banks of the Wai Tonga in Viti Levu, I noticed a number of its fruits floating in a sodden condition among the reeds at the river-side.

It is with the banyans that the dispersal of the seeds by frugivorous birds becomes most evident. This is at once indicated by the frequent occurrence of these trees in the interior of coral islets in the Western Pacific, as in Fiji and in the Solomon Islands. Fruit-pigeons roost in their branches, and birds shot on these islets often contain the fruits in their crops (*Bot. Chall. Exped.*, iv, 310). The process may also be seen in operation in Krakatoa. Professor Penzig found in 1897 that three species of Ficus had established themselves there since the eruption of 1883 through the agency of frugivorous birds. Besides pigeons, we find that parrots, hornbills, honey-eaters, &c., feed on these fruits, and I possess a large number of references to this subject. The Messrs. Layard in New Caledonia, Dr. Meyer in Celebes, Mr. Everett in Borneo, Dr. Forbes in Sumatra, and several other contributors to *Ibis* might be here mentioned. Dr. Beccari, in his *Wanderings in the Great Forests of Borneo*, speaks of " the facile dissemination of the various species of Ficus through the agency of birds," and he arrives at certain important conclusions which are discussed in Chapter XXXIII.

I have before alluded to the absence of Ficus from Hawaii. This group possesses the Honey-Eaters (Meliphagidæ), birds well suited for dispersing species of Ficus over Polynesia; but this family of birds is only represented by peculiar genera in Hawaii, and therein lies the explanation. At the time when the Honey-Eaters roamed over Polynesia, the genus Ficus had not arrived from Malaya. The connection between the bird and the plant is well shown on Fernando Noronha, which possesses a peculiar species of Ficus and a peculiar species of dove, the only fruit-eating bird in the island (Ridley).

The Absentees from Tahiti

Generally speaking, all the "difficult" genera which puzzle the student of plant-dispersal in Fiji and Hawaii are absent from the Tahitian region. Those with stone-fruits and with large seeds,

where the stone or seed is an inch in size and over, are absent from Tahiti. Thus the genera Canarium, Dracontomelon, Myristica, Sterculia, and others, of which the three first-named are known to be dispersed by fruit-pigeons, have not advanced into the Pacific eastward of the Fijian region. We miss in the Tahitian islands the large-fruited palms of Fiji, such as the Veitchias with fruits two to two and a half inches (5 to 6 cm.) long, and we find in their place a Ptychosperma, evidently very rare, and the widely spread Pritchardia pacifica, that may have been introduced by man, both with drupes not far exceeding half an inch (1·2 cm.) in size. The islands of the Tahitian region also lack the Coniferæ ; and genera like Dammara, Dacrydium, and Podocarpus that give such a character to the Fijian forests are not to be found. In this region we do not find many of the large-seeded Leguminous genera, such as Cynometra, Storckiella, and Afzelia, that occur in Fiji, the only large-seeded genera that it possesses being such as are brought by the currents, namely, Mucuna, Strongylodon, Cæsalpinia. The difficulties presented by the occurrence of the inland species of Canavalia and Mezoneuron in Hawaii do not offer themselves in Tahiti (see Chapter XV). Tahiti also lacks, as often before observed, the mangroves and most of the plants of the mangrove-formation.

As above remarked, the Fijian trees with large "stones" and heavy seeds an inch in size are not to be reckoned amongst the indigenous Tahitian plants, "size" being an important determining factor in the exclusion. The occurrence of Elæocarpus in Rarotonga presents no real difficulty, as I have explained in Chapter XXVI. An apparent exception is presented by the existence in Tahiti of Calophyllum spectabile, where the stones are about an inch across ; but since its fruits can float in sea-water for nearly a month, and on account of the value placed on its timber by the Polynesians, we cannot altogether exclude the agencies of man and the currents. One seeming exception is also offered by the presence of Serianthes myriadenia, a tree which in Fiji grows both in the forests and on the banks of the tidal estuaries. Its seeds, which are six to seven-tenths of an inch (15 to 18 mm.) in length, have no buoyancy, and the pods float only two or three weeks. The case of Lepinia tahitensis is alluded to elsewhere, but it may be added that these and other difficulties await further investigation.

A great many Fijian plants are not found in the Tahitian region, such as Micromelum, those of the order Meliaceæ, the Melastomaceous genus Medinilla, Myrmecodia, Ophiorrhiza, &c.,

which are often quite as well fitted for over-sea transport as are several of the plants already established there. But it should be remembered that crowding out would often come into play in such a contracted region. The area, however, has been very generously dealt with as regards plant genera. Though the total land-surface cannot be more than one-fourth or one-third that of Fiji or Hawaii, it possesses more than half the number of genera found in Fiji, and four-fifths of the number found in Hawaii.

Fiji

The Fijian Genera not found in either the Tahitian or Hawaiian Regions

We have already in some degree dealt with Fiji in so far as the partial dispersal of genera over the Pacific islands is concerned. We have seen that it possesses very few genera (not a score in all) in common with Hawaii that are not found in the Tahitian region, and it is assumed that in most cases such genera reached Hawaii independently and not through the South Pacific. On the other hand, excluding the grasses, sedges, and vascular cryptogams, Fiji owns in common with Tahiti between sixty and seventy genera that do not occur in Hawaii. This shows unmistakably the trend of plant migration in the Pacific islands. Several interesting features in plant-distribution have been already brought out, and notably the fact that Indo-Malayan genera with large seeds or "stones" an inch in size have been arrested in the Fijian region in their passage into the South Pacific. Thus Canarium, Dracontomelon, Myristica, and Sterculia have not extended eastward of the Fijian area.

Yet a very large proportion of the Fijian genera, quite half of the total number, are not represented either in the Tahitian or in the Hawaiian region ; and of many of them it is obvious that they are as well fitted to be carried over the Pacific as are those that have actually reached Tahiti and Hawaii. Take, for instance, Begonia, which has not extended east of Fiji, though Hillebrandia, a genus of the order, is peculiar to Hawaii. Nor can we explain why with three genera like Geissois, Dolicholobium, and Alstonia, possessing seeds dispersed by the winds, only the last-named has passed beyond Fiji. However, as before remarked, it is probable that lack of opportunity rather than capacity for dispersal has determined the matter, and we must, therefore, assume that many of the genera have

halted in the Fijian region because they entered the Pacific after the age of active general dispersal over that ocean.

Occasionally we notice in this region that which we have observed in the case of Cyrtandra in different Pacific groups, namely, a sudden development of what Hillebrand terms "formative energy" in a genus, such as we find in the case of Elatostema in Samoa, and in that of Psychotria in Fiji and Samoa. The principle of polymorphism in the development of species is also illustrated by Micromelum and by Limnanthemum. In the last case we possess a typical polymorphous species in Limnanthemum indicum that has played in this respect the *rôle* of Naias marina in the warm waters of the globe.

With several genera that like Gnetum, Myristica, and Sterculia occur both in the Old and the New World, it is evident that in explaining their distribution we are dealing with something more than questions of means of dispersal. With these genera, and with others like Lindenia, it seems almost futile to talk of means of dispersal, when to all appearance their existing distribution is but the remnant of an age of general dispersion over the greater part of the warm regions of the world. These genera, with others, might be cited in favour of the continental hypothesis relating to the islands of the Western Pacific. Trees with stone-fruits, such as Canarium, Couthovia, Dracontomelon, and Veitchia, where the stones are an inch and more in length, might be also adduced by some in evidence of this theory. But in these cases the lesson of Elæocarpus (Chapter XXVI) should always be remembered, since the "stones" of drupes may vary greatly in size amongst the different species of a genus, and species seemingly "impossible" from the standpoint of dispersal in one group may be represented in other groups by species where the size of the "stone" presents no difficulty in attributing the dispersal of the genus to frugivorous birds.

Sterculia

The problem connected with the presence of this genus in Fiji is but a part of the still more difficult problem connected with the dispersal of the genus over the tropics. The riddle presented by the Fijian species seems, indeed, difficult enough; but it merely presents in miniature the great mystery surrounding the whole genus. According to the *Index Kewensis* no other species have been found in oceanic islands except those occurring in the Western Pacific, as in Fiji, the New Hebrides, and New Caledonia, and most of these seem to be confined to those islands. We have

here a genus that repeats the Dammara difficulty of the Western Pacific.

The trees are common in places in the Vanua Levu forests, where the large, woody, open follicles may be seen lying in numbers on the ground, empty and in all stages of decay. The seeds of one species, near Sterculia vitiensis, were nearly an inch long and sank like stones. The unopened follicles will float for weeks ; but it is evident that Nature does not disperse the genus in this fashion, since the fruits before dehiscence remain on the tree. It is also noteworthy that Gaudichaud, when describing the floating drift of the Molucca seas, refers to the open follicles of two or three species of Sterculia (*Bot. Chall. Exped.*, iii, 279). The fruits never came under my notice in the drift of Fiji. The seeds of a Fijian species examined by me were four-fifths of an inch (2 cm.) long. They had a thin, brittle, outer skin and crustaceous inner test, and, being edible, might attract birds ; but such birds would be ground feeders, like the Megapod, and the Goura pigeon of New Guinea, and the Nicobar pigeon, birds of this habit being rare in Fiji. I should doubt whether the seeds are sufficiently protected to be preserved from injury in a bird's stomach during a long sea-passage ; and they may thus be placed in the same category with the seeds of Myristica, a genus that has also failed to reach Tahiti and Hawaii.

But the distribution of Sterculia raises other more important questions than that connected with its occurrence in Fiji, which involves an over-sea passage of only 500 or 600 miles. As in Podocarpus amongst the Coniferæ, which has a similar distribution in the Western Pacific, we have to explain the existence of the genus in the three great continental masses of Africa, Asia, and America, now separated by oceans several thousands of miles across. Here also we must look far back into the ages for a common centre of diffusion in the extreme north, such as is in a sense suggested by the occurrence of the order in the Eocene beds of Europe.

As showing unmistakably that Fiji received its species from the Old World, it may be observed that one of its trees, Sterculia vitiensis, is very closely allied to S. fœtida, widely spread in tropical Asia, in Malaya, and Australia, as well as in Africa.

Trichospermum (Sterculiaceæ)

There are only two species of this tree recorded in the *Index Kewensis*, one in Java, and one in Fiji as well as in Samoa. The

fruit is a capsule with small, flat seeds, margined by long hairs, that might possibly attach themselves to a bird's feathers.

Micromelum (Rutaceæ)

This small genus of tropical Asia, Malaya, tropical Australia and the islands of the Western Pacific, has one species, Micromelum pubescens, possessing the range of the genus with other species that are restricted to different localities. We thus have apparently another illustration of the part played by a wide-ranging polymorphous plant in providing new species. The red berries would easily attract frugivorous birds; but the seed-tests seem too delicate to allow the seeds to remain more than a few hours in a bird's stomach without injury.

Cananga odorata (Anonaceæ)

This tree, which is cultivated in many places in tropical Asia and Malaya, but is certainly indigenous, according to the authors of the *Flora Indica*, in Ava and Tenasserim, has apparently extended into the Pacific by cultivation. But though much valued by the natives on account of its fragrant flowers, and in consequence often planted by them near their villages, it grows in some localities in Fiji and Samoa as an indigenous plant. The berries are especially suited for dispersal by frugivorous birds, their flat seeds, 8 mm. in length, possessing hard crustaceous tests that would enable them to pass unharmed in a bird's droppings. According to Reinecke the fruits are sought after by pigeons, and particularly by Didunculus strigirostris, the Samoan Tooth-Billed Pigeon. The tree has not travelled eastward of Tonga and Samoa, with the exception of its occurrence in Rarotonga; and according to Mr. Cheeseman the Rarotongans received it from Samoa several years ago.

Geissois (Saxifragaceæ)

This genus of seven or eight known species is found in Australia, New Caledonia, the New Hebrides, and Fiji. Since New Caledonia possesses four species, it may be considered the home of the genus. To the Fijian endemic species, G. ternata, I paid special attention. The capsules dehisce on the tree and allow the small seeds to escape. These seeds, which are very light, 150 to 200 going to a grain, are 3 to 4 mm. long and are winged at one end. They could no doubt be carried some distance by strong

winds; but they possess no buoyancy. Large bats probably aid in their dispersal. The Fijians assert that these animals are in the habit of visiting the trees for the sake of the honey furnished by the conspicuous red flowers. When they see a bat flying towards these trees, they are wont to remark that it is going to drink the "se ni vota," that is, to suck the flowers of the Vota tree. It is very likely that seeds would sometimes be carried in their fur for considerable distances.

Begonia

Before the discovery of Hillebrandia, a new genus of the Begoniaceæ, in Hawaii, the order was not known from Polynesia. However, in 1878 Mr. Horne collected a species of Begonia in Fiji, and it was probably this species that frequently came under my notice in the rain-forests of the Vanua Levu mountains. In 1883 I collected a Begonia in the Solomon Islands, which I gave to Baron F. von Mueller, who informed me that it was the first record of the genus east of New Guinea, the description of Mr. Horne's Fijian plant apparently not having been published (see Guppy's *Solomon Islands*, p. 288). It is not easy to explain why a genus with such minute seeds, which are apparently as well fitted for dispersal as those of the orchids, should have such a limited distribution in the Pacific.

Dolicholobium (Rubiaceæ)

In the *Index Kewensis* this genus, containing five species, is restricted to Fiji. It must, however, be more generally distributed in the Western Pacific, since the genus was identified at Kew among my Solomon Island collections, and it is recorded in the list given in my book on that group (pages 283, 288, 297).

The showy, large, white, fragrant flowers of these small trees recall those of Lindenia, with which Dolicholobium is often associated in Fiji by the sides of streams and rivers. As Horne observes, the Fijian Dolicholobiums range from the sea-shores and the heads of the estuaries to the tops of the highest mountains. As noticed by me in the Solomon Islands they affected the same station, being especially common on the banks of streams. The genus has a long, narrow capsule six inches or more in length. The linear seeds, though very light, are an inch or more long, the coats being drawn out into a long tail at either end, and thus differing greatly from those of Lindenia, the other Rubiaceous genus, with which these plants are so frequently associated at the

river-side. I can only suppose that the seeds are transported by the winds. The history of the genus is suggested in my remarks on Lindenia.

Lindenia (Rubiaceæ)

Respecting its distribution in the Pacific, this genus of showy river-side shrubs takes the same place amongst the plants that Galaxias takes among the fishes. It is full of mystery. Of the four species known, two grow on the river-banks of Central America and two in similar stations in the islands of the Western Pacific. Of the last-named both occur in New Caledonia, one of them being endemic, whilst the other, Lindenia vitiensis, is found also in Fiji and Samoa. Reinecke seemingly records no Samoan species, but in the list of additions at the end of his *Flora Vitiensis*, Seemann refers to the Fijian species as having been found in Samoa by Dr. Graeffe.

Lindenia vitiensis, as Horne aptly remarks, adorns the rocky banks of many Fijian streams with its cream-coloured flowers, which impregnate the air with their sweet odour. I found it in Vanua Levu, both at the heads of the estuaries and beside the stream and the torrent in the heart of the mountains. It was often associated with a species of Dolicholobium, which it resembled strangely in its large, showy, scented flowers and in the form of the leaf. Seemann says it is also accompanied at the river-side in Viti Levu by Ficus bambusæfolia and Acalypha rivularis. It is noteworthy that all the four plants here mentioned as being associated river-side plants in Fiji possess the long, narrow leaves of the willow type, a subject that is discussed in note 79.

The capsules of Lindenia vitiensis contain numbers of small, angular seeds about 1·5 mm. across, some 400 of them when well dried going to a grain. The seeds float buoyantly by reason of their outer covering of crisp, air-bearing, cellular tissue. When this outer covering is stripped off, the minute nucleus, or seed proper, which is barely a millimetre across and is but slightly protected, sinks at once. As the seeds float on the surface of a stream they might readily get on the plumage of an aquatic bird; but they have no special means of attachment; though, if they dried on the feathers they might adhere to some extent. That they could be carried in mud adhering to a bird across an ocean's breadth I think most unlikely; and it should be remembered in this connection that only the dead or sickly seeds would be found at the bottom of a stream.

The most reasonable explanation of the extraordinary distribution of Lindenia is that it was in a past age found over the tropical regions of both America and the Old World, and that it has died out over the greater part of its original area. To study the means of dispersal of plants with such a distribution seems almost futile. I am inclined to think that the limited range of Dolicholobium, so frequently its station-companion in Fiji, may be similarly explained.

Limnanthemum (Gentianaceæ)

This interesting genus of aquatic plants is dispersed over the tropical and temperate regions of the globe, but with the exception of Fiji and the New Hebrides it is not found in oceanic groups, though it occurs in large continental islands like New Caledonia and Cuba. About twenty species are enumerated in the *Index Kewensis*, but it is stated in the *Genera Plantarum* that they can probably be reduced to ten, the reduction being chiefly applicable to the tropical species, nearly all of which are reducible to varieties of L. indicum, the temperate species being often very distinct. It would thus appear that although dispersal is still active in the tropics, it is in part suspended in the temperate zone, and we seem to possess in L. indicum a typical polymorphous species that has played the *rôle* of Naias marina in the warm, fresh waters of the globe (see page 368).

Although some of the temperate species, like Limnanthemum nymphæoides in Europe and Northern Asia, have a wide range, it is probable that this is connected not so much with means of dispersal, as with its relation to present and past drainage-areas. Rivers in the lapse of ages change their courses and carry their aquatic floras with them, leaving, however, a few of their plants around the springs and in the lakes which serve still as centres of dispersal. Rivers may even exchange their plants in flood-time in extensive level districts. Nor is the occurrence of the genus in the Old and New Worlds in the northern hemisphere to be connected with questions of dispersal across an ocean. Except in the case of small-seeded plants, like Nasturtium and Lythrum, where the dispersal could be carried on by water-fowl, the plant-species being often identical on both sides of the Atlantic, it is probable that most of the large-seeded river-side genera common to Europe and North America, such as Iris and Acorus, had in past ages their home in the extreme north, whence the plants spread as from a

focus into the continents of America and Eurasia. It is also to be doubted whether even in the tropics there has been much over-sea dispersal of Limnanthemum without the aid of man, and reasons will be given for the belief that probably in Fiji, in the New Hebrides, and in New Caledonia the seeds of the first plants were unintentionally introduced by the aborigines.

Following Bentham we may regard the species of the Western Pacific Islands as a form of the wide-ranging Limnanthemum indicum. These plants in Fiji do not play the part in river-vegetation that they do in the temperate regions, as for instance in the Upper Thames. They are not common except in places, and seem to be chiefly confined to Viti Levu, particularly to ponds in the Rewa delta, where their *rôle* is that of an Indian tank plant. In the Rewa delta they may be sometimes seen thriving in brackish water having a density of 1·005.

Looking at the mode of dispersal to which the Limnanthemums owe their existence in the Western Pacific, we cannot disregard, especially in Fiji, the possibility of the seeds having been unintentionally transported by the natives when they carried in their migrations their edible tubers, such as Colocasia antiquorum, Alocasia indica, and Cyrtosperma edulis, that are cultivated in wet places. It is in the ponds around which these plants grow that the Limnanthemums thrive. The Chinese, with their peculiar methods of cultivation, are now carrying with them strange water-plants over the warmer regions of the globe; and it would be surprising if the Pacific islanders in their migrations did not do the same. If such an introduction, however, took place, it must have happened before the time of Captain Cook, when the plant was found in New Caledonia. (It may be remarked in this connection that the seeds of the genus will germinate after being kept dry for years. Seeds of the British species which I had kept dry for two and a half years germinated healthily when placed in water.)

Some years ago I ascertained that the seeds of the British plants were enabled, by means of their fringe of hairs, to attach themselves firmly to the downy plumage of a bird's breast. This could not happen with the Fijian plant as the seeds are naked, and the same may be said of some species described by Gray and Chapman as widely spread over the United States. The seeds of the genus appear quite unsuited for safe transport inside the body of a bird. The Fijians give the plants a variety of names, nearly all of which are associated with the word for a duck, and none of them bear an ancient impress. Thus we find such names as

"Ndambe-ndambe-ni-nga" and "Vothe-vothe-ni-nga," meaning respectively "the duck's seat" and "the duck's paddle."

Ceratophyllum demersum

This wonderful aquatic has been dispersed over most of the globe; but I will only mention its occurrence in oceanic islands, such as Fiji, Samoa, the Bermudas, and the Azores, to indicate the necessity of attributing its distribution in islands to birds. Several years ago I made a careful study in England of the habits and mode of germination of this plant, the results of which are given in *Science Gossip* for November, 1894; but reference can only be made here to such points as bear on the occurrence of the plant in the Pacific islands.

It is well known that in our English ponds and rivers the plant propagates itself, as a rule, by budding; and that it is only in unusually hot and dry summers, such as that of 1893, when many ponds became very low and were excessively heated, that the fruits mature in any quantity. My observations clearly showed that a higher temperature is required for the completion of maturation than for the early stage of the fruiting process and for the flowering. After a comparison of my river and pond temperatures, I formed the conclusion that whilst in water 12 to 18 inches deep this plant requires for a week or more an average daily maximum water temperature of 70° F. to produce its flowers, a warmth of 80° and over is necessary to mature its fruit, a condition to be found in England only in shallow ponds, where the plants may fruit abundantly, but not in rivers, where they flower and rarely mature the fruit (see also for the thermometric conditions my paper in *Proc. Roy. Phys. Soc. Edin.*, xii, 296). Since a yet lower temperature (an average maximum water temperature of 66° for a week or more) is sufficient for germination, it follows that the thermal conditions of our English climate will allow Ceratophyllum to germinate and to flower, though but rarely to mature the fruit.

Even in Fiji we can notice the distinction between the cooler river and the superheated ponds and swamps of the Rewa delta as regards the maturation of the fruit. In 1897 I found Ceratophyllum thriving in the main channel of the Lower Rewa where the water was quite fresh; whilst lower down where the water was often brackish its place was taken by Ruppia maritima. In the main river, where the water unmixed with sea-water rarely acquires

a temperature of 80° F., the reading being usually 78° to 79°, I never found the plants in fruit, and it is only in the superheated shallow waters of the swamps and back-waters that they mature their fruits.

Since Ceratophyllum even in tropical climates would probably only mature its fruits in the superheated waters of shallow ponds, tanks, and ditches, it follows that its dispersal by birds is confined to warm regions. In the cold waters of the Siberian lakes and rivers it would never mature its seeds, and could only be propagated by budding. If it existed in the head-springs of the sources of a river in these latitudes, it would be distributed by means of its floating shoots and fragments along the length of the river basin, and in the times of flood it might pass in the lower plains from one river system to another. When rivers changed their courses it would be left behind in the lakes and ponds and springs, and would also be carried away to the new region. In this manner it would in the course of ages be distributed over a continent without the aid of seed, propagating itself in a vegetative fashion.

In the case of oceanic islands, however, we have to appeal to the seed. Since the fruits sink in sea-water even after prolonged drying, and since a few days' immersion in sea-water, as I found, kills the floating plant, we are driven to the agency of birds. The fruits, which without appendages are a quarter of an inch (6 mm.) in length, are too large and heavy to be carried in dry mud adhering to birds. The chances of their becoming entangled in a bird's feathers by means of their basal spines and terminal style seem small, since they would be lying usually on the mud under the water. They are quite fitted for safe transport in the stomach and intestines of birds, such as is established in Chapter XXXIII for Potamogeton and Sparganium in the case of ducks. As my experiments show, drying for a period of three months does not injure the germinating capacity of the seeds.

Dracontomelon (Anacardiaceæ)

This is a genus accredited in the *Index Kewensis* with eight species, of which three belong to Borneo, one to Sumatra, one to Java, one to the Philippines, and two to Fiji, all the species being restricted in their range. My observations were confined to D. vitiense, Engler (D. sylvestre in Seemann's work), the Tarawau of the Fijians, who regard it as a tree that is planted by the dead in Naithombothombo, the place of departed spirits, according to the

legend given by Hazlewood in his Fijian Dictionary. Its method of dissemination in the Fijian forests is, however, far more prosaic. Pigs and fruit-pigeons assist in the dispersal of the seeds in these islands. Pigs are often found in the vicinity of a Tarawau tree; and evidently they much appreciate the fallen fleshy fruits, which are about $1\frac{1}{3}$ inch (3·3 cm.) across and inclose a large stone $\frac{7}{8}$ inch (2·2 cm.) in diameter. The entire fruit and the detached stone sink in sea-water, the last floating only a few hours, even after drying for four years. Mr. Hemsley regards the genus as probably dispersed by the currents, since a stone was found amongst the floating drift collected by the *Challenger* Expedition off the coast of New Guinea. The stone, however, is described as seedless, which may explain its buoyancy. It is, however, to the fruit-pigeon that we must look for the dispersal of this genus. In the crop of one of these birds shot in Fiji I found the entire fruit of a Tarawau tree.

Canarium (Burseraceæ)

This genus of trees, to which nearly a hundred species are referred in the *Index Kewensis*, belongs mainly to tropical Asia and Malaya, a few species occurring in tropical Africa, Madagascar, the Mascarene Islands, and Polynesia. Its great home is in Malaya, to which two-thirds of the species are confined; but its distribution in the oceanic islands of the Indian and Pacific Oceans is especially interesting, Mauritius, Bourbon, Fiji, Tonga, and Samoa (Horne) each possessing a species.

The large drupes of the genus, as I found in Fiji, have no capacity for dispersal by currents; and we are, therefore, compelled to appeal to the agency of the frugivorous bird. Yet to a person unaccustomed to the ways of fruit-pigeons the transportation across a broad tract of ocean of large heavy "stones," an inch and more in size, would seem impossible; and even to a student of dispersal improbable. Unless, however, we prefer to accept the Lemurian theory for the Indian Ocean and the theory of a Melanesian continent for the Pacific we are compelled to appeal to these birds; and it can scarcely be said that our appeal is without some justification. Both in the Solomon Islands and in the Fijis I was familiar with the dispersal of the stones of these trees by fruit-pigeons; and Wallace, amongst other writers, observed the same long ago in the Malayan Islands (*Malay Archipelago*). Stones obtained from the crops of Fijian pigeons measured $1\frac{2}{10} \times 1$ inch (3 × 2·5 cm.). In the Solomon Islands these birds stock the

interior of the coral islets with trees of the genus, and the ground below the trees is often strewn with the disgorged stones (*Bot. Chall. Exped.*, iv, 310; Guppy's *Solomon Islands*, p. 85).

Although the difficulty concerned with the transport of the seeds across a broad tract of ocean seems very great, it is quite possible that further investigation will enable us to overcome this objection, just as we have done in Chapter XXVI when explaining how the genus Elæocarpus may have reached Hawaii. It is, indeed, not unlikely that, as with Elæocarpus, the stones of the drupes may in some species be much smaller and far more fitted for being carried in a bird's body over several hundred miles of ocean.

Couthovia (Loganiaceæ)

Reference is here made to this genus because its mode of dispersal is known, and because I was familiar with it in Fiji. Seemann gives two species for Fiji, C. corynocarpa and C. seemanni, and the few other species known seem to be confined to the Western Pacific. Solereder gives a third species, C. densiflora, for Kaiser-Wilhelmsland in New Guinea (Engler's *Pflanz. Fam.* teil 4, abth. 2); and a Solomon Island species, nearly allied to, if not a variety of, the Fijian species, C. seemanni, is referred to in the list of plants from that group given in my book on those islands. I found C. corynocarpa not infrequently growing on the banks of small rivers in the heart of Vanua Levu. Its drupes, which float for a few days in sea-water, are, according to Seemann, eaten by fruit-pigeons. The "stone" varies from 2 to 4 centimetres ($\frac{3}{4}$—$1\frac{1}{2}$ inch) in length; and from the standpoint of dispersal the genus ranks with Canarium and Dracontomelon. Seemann describes and figures this species, which was constituted by Gray, in his *Flora Vitiensis;* but, apparently through an error, it is in the *Index Kewensis* accredited to Hawaii. Hillebrand makes no reference to the genus in his book on the Hawaiian flora.

Veitchia (Palmaceæ)

This genus of palms is closely allied to Ptychosperma, a Malayan genus also represented in Fiji. The *Index Kewensis* names four species, one New Hebridean, and three Fijian. The fruits of two of the last-named species tested by me had no floating power. The seed is about an inch long, and the genus would be likely to be spread by fruit-pigeons. From the standpoint of dispersal the genus would be placed with Canarium and Couthovia; but possibly

its presence in the Pacific may be indicative of an ancient Western Pacific continent.

Hibbertia (Dilleniaceæ)

This genus of some eighty known species is almost entirely Australian, with the exception of a few species found in New Caledonia, Tasmania, and apparently also in the Mascarene Islands. Horne was the first to record a species from Fiji, where it grows commonly in the "talasinga" plains on the lee sides of the islands, and also on the scantily vegetated mountain summits. In Vanua Levu I often found these plants growing on the rocky peaks of the highest mountains of the island, as on Mbatini, 3,500 feet, and on Mariko, 2,900 feet. Their presence on these isolated peaks can only be attributed to birds. The carpels contain one or two seeds, which have a membranous aril; but in the plains the seeds are usually destroyed by grubs.

Myrmecodia and *Hydnophytum* (Rubiaceæ)

These two genera of epiphytes, distributed over Malaya and extending to the islands of the Western Pacific, possess tuber-like stems, which are extensively chambered by ants that find a home in the interior. They were familiar to me in the Solomon Islands, where they frequently grow on the mangroves and on other littoral trees. They do not form such a feature in the shore vegetation of Fiji, and judging from the observations of Dr. Seemann and myself they occur most often on the wooded mountain-peaks. The berries of these plants would attract frugivorous birds; and their pyrenes, which in a Fijian Myrmecodia I found to be 4 millimetres long, appear quite suitable for dispersal through this agency. It would seem that germination may occur in the berry on the plant. A specimen of Myrmecodia in fruit, that had been lying overlooked for a fortnight between newspapers during one of my mountain journeys, displayed on examination the pyrenes in a germinating condition, the process being subsequently completed. The reader will find these interesting plants described and illustrated in the English edition of Schimper's work on *Plant-Geography*, pp. 149, 150.

Myristica

The Nutmeg trees, though principally at home in Indo-Malaya, are found also in the warm regions of Africa and America, as well

as in the islands of the Western Pacific from the Solomon group eastward to Fiji, Tonga, and Samoa. The Tongan and Samoan groups possess two species in common, whilst Fiji seems to possess its own species, four or five in number.

The seeds of this genus have long been known to be dispersed by fruit-pigeons. Mr. Moseley, in his *Notes of a Naturalist*, and in the *Journal of the Linnean Society* (vol. xv), tells us how at one time these birds in their dissemination of the seeds in the Banda Islands were active opponents of the policy of the Dutch Government in preserving their monopoly of the cultivation of the nutmeg of commerce. He found numbers of wild nutmegs in the crops of these birds in the Admiralty Islands, some of which were partially digested and others seemingly sound; and Mr. Hemsley includes the genus as amongst those dispersed in the Western Pacific by birds (*Bot. Chall. Exped.*, Introd. 46; iv, 229, 308). In my book on the Solomon Islands I refer to the occurrence of these seeds in the crops of fruit-pigeons; and I found that the seeds were similarly dispersed by these birds in Fiji. It is likely that the absence of the genus from Eastern Polynesia is to be partially connected with the insufficient protection of the seeds against injury during such a long ocean passage in a bird's body.

Gaudichaud, as quoted by Hemsley, refers to the occurrence of the fruits of three or four species of Myristica in the drift floating in the Molucca Sea. When in the Solomon Islands I noticed that the unopened fruits of a species floated in sea-water. In later years in Fiji I tested this point, and found that whilst the fruits just before dehiscing will float between three and seven days in sea-water, the seeds sink. As I have pointed out in the chapter on Drift, rivers carry down to the sea an abundance of seeds and fruits that can float a few days but do not imply dispersal by currents.

Although, as I have above remarked, the localised range of the genus in Polynesia may be in part connected with the insufficient protection of the seed, it is apparent that in the case of a genus found in Asia, Africa, and America we are brought into contact with questions other than those of means of dispersal. No one would pretend that Myristica seeds could be carried by birds uninjured across the Pacific Ocean; and to explain the present distribution of the genus we must recall cases of a similar kind, such as Podocarpus, where the genus in past ages had a home in the north, from which, as from a focus of dispersion, it extended into the continents of the Old and the New World (see p. 302).

Rhaphidophora (Araceæ)

This genus of climbing aroids, which gives a character to the forests of Indo-Malaya as well as to those of the Western Pacific, is represented in the New Hebrides, Fiji, Tonga, and Rarotonga by a variety of the widely spread R. pertusa that ranges over Indo-Malaya and Eastern Australia. The ripe berries would readily attract birds; and the seeds, 4·5 millimetres long in the case of a Fijian plant, appear hard enough to pass unharmed through a bird's digestive canal. We seem here to have evidence of a somewhat recent connection between Indo-Malaya and Polynesia through the agency of frugivorous birds. That the genus has been long established in Polynesia is, however, indicated by the occurrence there of a species seemingly peculiar to Fiji. We are disappointed that in Engler's recent contribution to the *Pflanzenreich* (in his volume on the Araceæ-Pothoideæ) he has not been able to include this genus in the field of his studies.

Gnetum (Gnetaceæ)

This Gymnospermous genus, which is found in the warm regions both of the Old and the New World, is represented in Fiji by a Malayan species, Gnetum gnemon, which exists also in the Solomon group with other species of the genus (Guppy's *Solomon Islands*, pp. 288, 301). I was familiar with this species in both Fiji and the Solomon group; but in the first-named locality it is seemingly restricted to the borders of Wainunu Bay on the south side of Vanua Levu, where Dr. Harvey first found it. It grows there abundantly in young wood.

It seems almost idle to discuss the mode of dispersal of a genus that is placed in a class apart with the African Welwitschia and the European Ephedra, possessing with them a history of which we know nothing. Yet it is ranked by Mr. Hemsley amongst those genera that are dispersed in Polynesia by birds, and he produces better evidence in support of this view than we possess for many other plants. Thus a fruit of a species of Gnetum, perhaps G. gnemon, has been found in a New Guinea fruit-pigeon; and the fruits of two species of the genus were found in the crops of fruit-pigeons shot by Mr. Moseley in the Admiralty Islands (*Bot. Chall. Exped.*, Introd. 46; iv, 308). The red drupes of Gnetum gnemon of Fiji would readily attract birds, and their nut-like stones, about 8 millimetres long, are well suited for this

mode of dispersal. My experiments in Fiji show that neither the drupe nor the stone of this species floats in sea-water; and it is probable that the fruits of this genus referred to by Mr. Hemsley as having been picked up on the beach in the Aru Islands possessed only a temporary buoyancy.

This genus presents us with the same puzzling question put to us by several Fijian genera, such as Myristica and Podocarpus, that occur in both Asia and America; and until we answer that query it seems almost futile to study modes of dispersal.

Elatostema (Urticaceæ)

This genus of annual and perennial herbs belongs to the tropical regions of the Old World. It is represented in Samoa by fifteen known species and by at least four or five in Fiji, whilst with the exception of a solitary Tahitian species it is not recorded from East Polynesia. Reference is here made to it particularly on account of its great development in Samoa. We have here a genus that, like Psychotria in Fiji and Cyrtandra in Fiji, Samoa, and Hawaii, runs riot in respect to the production of species (see p. 317). Dr. Reinecke describes fifteen Samoan species, of which, with the exception of two found in Malaya, all seem to be described for the first time. So sensitive, he remarks, is the genus to external conditions that station-forms abound; and he points out that if we were to follow the dividing lines usually recognised between species, we should account every station-form a new species. It is, of course, obvious that the polymorphism of the Samoan Elatostemas depends primarily not on the varying influence of station but on their sensitiveness to external conditions. One might put the question to the Samoan Elatostemas that Hillebrand put to the Hawaiian Cyrtandras, and ask why nature in this particular genus in this particular locality thus luxuriates in formative energy. Almost every Pacific group in respect of some of its plants presents the problem so well stated by Dr. Reinecke for this genus in Samoa. It is noteworthy that Schimper, in his work on *Plant-Geography* (English edition, pp. 291, 297, 299), especially singles out Elatostema and Cyrtandra as growing socially in the tropical rain-forests of Java and of the Asiatic mainland.

Scirpodendron costatum (Cyperaceæ)

As far as I can gather, this giant-sedge has not been previously recorded from Fiji; but it is included in the Samoan flora, and has

also been found at Penang and Singapore, as well as in Borneo, Java, and Queensland. In Samoa, as we learn from Reinecke, it grows both in the coast swamps and on dry ground. In Fiji it is very common in the mangrove-swamps at the mouths of rivers, especially in the Lower Rewa; but in Vanua Levu it is also frequent in the marshy localities of inland plateaux, 700 to 800 feet above the sea, as well as by the side of streams in swampy districts on the lower hill slopes. This double station in the salt-water swamp of the coast and in the fresh-water marsh of the interior seems to be repeated in Java, where the plant was first discovered by Zippelius on the banks of torrents in mountainous regions and in swampy places.

The genus comprises, according to the *Index Kewensis*, only this species, though variations are to be observed in plants from different localities. The species was described by Kurz in the *Journal of the Asiatic Society of Bengal* (vol. 38, 1869) and by Bentham in his *Flora Australiensis*; and an illustration is given by Miquel in his *Illustrations de la Flore de l'Archipel Indien* (1871). The plant is so common in Fiji that one can only suppose that its resemblance to a stemless Pandanus, from which, as Kurz observes, it is with difficulty distinguished except when in flower or fruit, led to its being overlooked by both Seemann and Horne. Its leaves, from 9 to 12 feet in length, are commonly used for making mats and for thatching, both in Fiji and Samoa. The plant usually attains a height of 3 to 5 feet.

The fruits occur abundantly in the floating and stranded river and sea drift in Fiji, a circumstance that led to my discovery of the parent plant in the swamps. The fruit, which is about half an inch (12 mm.) long, consists of a hard, stony nut invested by a thick ribbed cork-like covering, to which it owes its buoyancy, since the nut sinks. The detached fruit is perforated at the base through both coverings, and only a little soft tissue closes the aperture in the inner shell, the protection against the entry of sea-water in the case of floating fruits being quite inadequate. This explains also why the stranded fruits were so frequently found by me germinating on the beach, where, as my observations showed, they never established the plant. This early germination would prove to be an advantage in the case of fruits stranded in a suitable locality.

But though the perforation in the fruit favours its early germination, it lessens its ability to withstand a long sea-passage without injury to the embryo. I found in different experiments on

fruits of plants growing in the mangrove swamps, that when placed in sea-water 40 per cent. sank during the first fortnight, whilst 15 per cent. floated after five or six weeks, but all were at the bottom in two months. On the other hand, fruits from plants of the swamps of the inland plateaux displayed much feebler floating power, in some cases sinking at once, in others floating for a few days, and in others again floating for a week or two. In this case the outer cork-like covering proved to have lost most of its floating power.

From the number of empty seed-vessels found, both in the floating and stranded drift, it appeared evident that the seed had often rotted away during the flotation. It is apparent from these observations and experiments that Scirpodendron costatum is not suited for dispersal by currents over wide tracts of ocean. The fruits might be able to float unharmed for a few weeks, but they would be unable to accomplish much more than the 500 or 600 miles intervening between Fiji and the nearest groups to the west.

Lemnaceæ

This order, judging from the writings of Hegelmaier, Schenck, and Hemsley, is represented by one or other of the common species, Lemna minor, L. gibba, L. polyrrhiza, in various Atlantic islands, as in the Bermudas, the Azores, Madeira, the Canary Islands, and St. Helena; but doubts frequently arise as to their being truly indigenous. Lemna trisulca is regarded by Hemsley as indigenous in the Bermudas. Lemna minor has been introduced in recent years into Hawaii, where I observed it flowering and sometimes fruiting abundantly in the heated waters of the ponds. Two species found in other regions were recorded by Seemann from Fiji, and I have come upon few other records of the occurrence of the order in the tropical islands of the open Pacific. I am inclined to the opinion, based not only on the facts of distribution, but also on the results of numerous experiments on the means of dispersal, that this order has in most cases reached oceanic islands with man's assistance.

Some years ago I made a systematic study of the habits of the British Lemnæ, most of the results being published in the *Linnean Society's Journal* (vols. xxix and xxx), as far as concerned Lemna minor, L. gibba, and L. polyrrhiza. During this inquiry I ascertained that with these species, as well as with L. trisulca, the chances of a bird's carrying their fronds uninjured in its plumage

over a wide extent of ocean were small. None of them survived twenty-four hours' drying in fine weather, whether in the sun or in the shade; but in rainy weather they withstand an exposure of one or two days. It is, therefore, unlikely, even if the fronds were entangled by their rootlets in a bird's feathers, that they would be able under ordinary conditions to reproduce the plants after a day's flight of some five hundred miles across the sea. It must also be remembered that the drying capacity of the air when a bird is in full flight in ordinary weather would be that displayed during a gale of wind with a velocity of at least thirty to forty miles an hour. For this reason I do not think with Kerner that under usual conditions drops of water would be a factor of importance in causing the adherence of minute seeds of any kind to birds' plumage. Where the seeds are not available, it is most probable that birds disperse the duckweeds by their fronds over short distances, but not across broad seas. This would certainly apply to temperate latitudes, where these plants rarely seed. Thus with Lemna, as with Ceratophyllum, it would seem that the dispersal of the seeds by birds takes place normally only in warm latitudes. Those of the duckweeds could be transported in adherent mud over land-areas.

According to Hegelmaier, the two species of Lemna found in Fiji are L. paucicostata, an Asiatic species, and a variety of an Australian species, L. oligorrhiza, possessing dark root-sheaths. These plants mostly came under my notice in the Rewa delta. They were rarely seen in Vanua Levu, where in one locality I found the typical Lemna minor. The first species is also Samoan.

In 1897 and in 1899, in a pool near Notho in the Rewa delta, in Viti Levu, Fiji, I found a great abundance of a species of Wolffia, specimens of which were sent to Prof. Schimper with my mangrove collections, but his death intervened, and I have not been able to follow up the matter. On comparing the specimens with Hegelmaier's descriptions and plates, it would seem that the species is near W. arrhiza and W. brasiliensis, but differs from both in the greater length of the fronds. As concerning the means of dispersal of the genus, I may add that the fronds were killed after being allowed to dry for eighteen hours.

Marsilea (Marsileaceæ)

A species of this genus, apparently near Marsilea villosa, was common in the ditches and ponds around Notho, in the Rewa

delta, Fiji, in 1897–99. The genus is included by Horne in his list of Fijian plants; but is not given by Seemann. The villous sporocarps, when dry, are very light and readily catch in cloth and in feathers. Hillebrand includes in the Hawaiian flora M. villosa and M. crenulata. The first-named, which was collected by Chamisso and Gaudichaud, finds (he says on the authority of Braun) its nearest relative in a species from Oregon and California. The other has been collected in the Liukiu Islands, the Philippines, Mauritius, and Bourbon. It is very probable that the occurrence of the genus in oceanic islands is due to the agency of birds.

Summary of the Chapter

(1) We are here concerned with the more restricted distribution of non-endemic tropical genera over the Pacific. The general trend eastward of these genera is well brought out in the fact that whilst Fiji possesses some sixty or seventy genera in common with Tahiti to the exclusion of Hawaii, it does not possess a score in common with Hawaii to the exclusion of Tahiti. The grasses and sedges and the mountain genera are not here included; and we are comparing the flora of the Hawaiian lowlands below 4,000 feet with the floras in mass of Fiji and Tahiti.

(2) Hawaii possesses very few genera (less than thirty) that are not found either in Fiji or in Tahiti, or in both; and of these quite a third are to be traced to America.

(3) From two of these genera, Embelia, a land genus, and Naias, an aquatic genus, we obtain two important indications, namely, that specific differentiation has taken place to much the same extent in a water plant as in a land plant, whether in a continent or in an island. In other words, new species have been developed or are developing independently of the immediate environment and of isolating influences.

(4) The interchange of plants between the regions of Hawaii and Tahiti to the exclusion of Fiji has been very slight. Probably not half a dozen genera belong to this category.

(5) Excluding plants brought by man and by the currents, Tahiti possesses very few that present any difficulty from the standpoint of dispersal, plants with seeds or "stones" an inch in size being, as a rule, absent.

(6) With the genera (60—70) common to Fiji and Tahiti, and distributed, therefore, over the South Pacific, the wide-ranging

highly variable plant is an important factor in the development of peculiar species in the different groups, just as it has been shown to be in the previous chapter in the case of genera dispersed over the whole Pacific. The *rôle* of the polymorphous species has always been an important one in this region.

(7) In the case of several Fijian genera it seems almost futile to talk of existing means of dispersal, since the present distribution of genera like Sterculia and Gnetum, that occur on both sides of the Pacific, in America and in Asia, is not to be thus explained.

(8) On account of the large size of their seeds and "stones" it might be argued that certain of the Fijian plants afford evidence of a previous continental condition of the islands of the Western Pacific, since it is not easy to understand how such large seeds and "stones" could have been transported over broad seas by birds. It is, however, pointed out that in these respects the species of a genus may vary greatly, and that the seeds and stones may be large in some species and small in others.

(9) The greater number of the genera that have entered the Pacific from the Old World have not advanced eastward of the Fijian region, half of the Fijian genera not occurring in the Hawaiian and Tahitian regions; and the explanation of this is to be found not in any lack of capacities for dispersal, but in a want of opportunities. The story of plant-distribution in the Pacific is bound up with the successive stages of decreasing activity in the dispersing agencies. The area of active dispersion that at first comprised the whole of the tropical Pacific was afterwards restricted to the South Pacific, and finally to the Western Pacific only. The birds that in an early age carried seeds all over this ocean became more and more restricted in their ranges, probably on account of increasing diversity of climatic conditions. The plants of necessity responded to the ever narrowing conditions of bird-life in this ocean, and the differentiation of the plant and of the bird have taken place together.

CHAPTER XXVIII

THE POLYNESIAN AND HIS PLANTS

Identity of the problems presented by the indigenous plants and the peoples of the Pacific islands.—The food-plants of the Polynesians and the pre-Polynesians.—Their weeds.—The aboriginal weeds.—The white man's weeds.—Weeds follow the cultivator but are distributed by birds.—The general dispersion of weeds antedates the appearance of the Polynesian in the Pacific.—Weeds of little value to the ethnologist.—Aleurites moluccana.—Inocarpus edulis, Gyrocarpus Jacquini, Serianthes myriadenia, Leucæna Forsteri, Mussænda frondosa, Luffa insularum.—Summary.

Man and the Seed

Man in his distribution in the islands of the Pacific reproduces in a minor degree nearly all the difficulties presented there by plants, birds, and other forms of animal life. Like the plant he entered the ocean from the west; and as with the plants, so with the aborigines, there was an era of general dispersion over this ocean, followed by an age in which Polynesian man, ceasing to migrate, tended to settle down in the several groups, there undergoing differentiation in various respects, as in physical characters, in language, and in manners. Just as we can now recognise the type of a plant, of a bird, or of an insect, that belongs to a particular group of islands, so we can distinguish between the Hawaiian, the Tahitian, and the Maori, whether in physical characters, in his speech, or in his customs. Fiji possesses in the Papuan element of its Melanesian population the earliest type of man in the Pacific, just as it also possesses in the Coniferæ the most ancient types of trees in this region. Divesting his mind of all previous conceptions, the ethnologist, as I have remarked in my discussion of the distribution of Freycinetia in Chapter XXV, might profitably study *de novo* the dispersion of man in the Pacific from the standpoint of plant-dispersal.

Man and the seed have battled their way over the Pacific apparently in defiance of the prevailing winds and currents, and both have failed to reach the New World. Man in the Pacific is almost as enigmatical as the plant. As a denizen of this region he is by no means a recent introduction ; and though his food-plants are mainly Asiatic, they belong to distinct ages in the history of man's occupation of these islands.

I venture to think that a great deal lies behind the Indo-Malayan mask of the Polynesian, and that there is a story concerned with his origin that has yet to be told. We have by no means solved the riddle when by following the evidence we assign to him a home in Asia. It is only then that the real difficulties begin. It required many centuries of European civilisation for the discovery of America ; but the voyages of Columbus sink into insignificance when we reflect on what had been dared and accomplished by uncivilised man when he first landed on the shores of Hawaii and Tahiti.

The problem of man in the Pacific bristles with difficulties differing in degree but not in kind from those relating to the flora. Whenever a particular theory seems on the point of being well established, some disturbing question arises, and as with the plant, we are never able to push our facts quite home. Since I first visited the Solomon Islands, now twenty-four years ago, the Pacific islander and his flora have deeply interested me. The history of man and of the plant cannot be separated in the Pacific ; and the same determining principles of distribution have affected both.

The Food-Plants of the Polynesians and Pre-Polynesians

One can imperfectly distinguish two sets of food-plants in this region ; the first comprising such plants as Pachyrrhizus trilobus, Tacca pinnatifida, Amorphophallus campanulatus, the Mountain Bananas, the Wild Yams, and several others that grow wild, and, as a rule, only serve as food in times of scarcity ; the second including the plants that are extensively cultivated by the present islanders, such as the Breadfruit, the Banana (Musa paradisiaca), the Taro (Colocasia antiquorum) and the two Yams (Dioscorea alata and D. sativa), &c. Those of the first set probably formed the food of the earliest inhabitants of the Pacific Islands, pre-Polynesian peoples that practised only a rude sort of cultivation, as with the present " bush-men " of the islands of the Western Pacific. Those

of the second set belong to the later occupants of these islands, the Polynesians.

(a) *The Pre-Polynesian food-plants.*—In addition to those above named one may mention Cycas circinalis, Cyrtosperma edulis, Lablab vulgaris, Pandanus odoratissimus, Saccharum officinarum, Sagus vitiensis, &c. Inocarpus edulis is probably to be here included, and amongst the Wild Yams should be named Dioscorea nummularia and D. pentaphylla. Some of them are now occasionally cultivated ; but most of them only occur in the wild condition, either as weeds or as larger plants growing spontaneously in uncultivated localities. Even the knowledge of them as food-plants has sometimes been altogether lost, the present inhabitants of the Fijis, for instance, knowing nothing of Lablab vulgaris and Sagus vitiensis as sources of food. The question of the antiquity of the Coco-nut Palm in Polynesia was discussed at length by Seemann ; but for various reasons we cannot be absolutely certain whether or not it is an older denizen of the Pacific islands than the Polynesian. It is, however, to be inferred that it came originally from the home of the genus in America, perhaps as a gift brought by the Equatorial Current from the New World to Asia. Several chapters might be devoted to the discussion of the earlier food-plants of these islanders ; but here only a brief reference can be made to a few of them.

Perhaps the oldest of the earliest aboriginal food-plants are those that, like Cyrtosperma edulis and Sagus vitiensis, are apparently confined to Fiji. Here we seem to possess indications of the development of new species since that group was first occupied by man. Others, like Pachyrrhizus trilobus and Cycas circinalis, that are restricted to the groups of the Western Pacific may come next in relative antiquity.

Although most of the early food-plants hail from the Old World, the home of Pachyrrhizus is in America. One may indeed wonder how a plant with such a history ever reached the Western Pacific. It seems to be generally distributed in this part of the ocean, having been recorded from New Caledonia, the New Hebrides, Fiji, Tonga, and Samoa. Although its edible roots are only used in times of scarcity, the plant grows wild all over Fiji, being especially frequent in the "talasinga" plains. Though I searched diligently, it never presented me with its seed. In Tonga, according to Graeffe (as quoted by Reinecke) the plant is much employed in preparing the land for yam-cultivation, since it restrains the growth of weeds and keeps the soil moist.

Amongst the food-plants of this early period that are distributed over the South Pacific as far east as Tahiti may be mentioned the Wild Yams (D. nummularia and D. pentaphylla), the Mountain Bananas, Tacca pinnatifida, Amorphophallus campanulatus, and others. Of these Tacca pinnatifida and Dioscorea pentaphylla are alone found in Hawaii. I will only now refer to the Mountain Bananas.

The Mountain Bananas of the tropical South Pacific, distinguished by their erect fruit bunches and their seeded fruits, present us with one of the mysteries connected with aboriginal man in this ocean. Whether in New Caledonia, Fiji, Samoa, Rarotonga, or in Tahiti, they grow wild in the interior, and form often a conspicuous feature of the vegetation in the mountains and at the heads of the valleys. They are occasionally cultivated. Their Fijian and Samoan names of "Soanga" and "Soa'a" reproduce the names of the banana, "Saguing" and "Saing" in the Tagalog language of the Philippine Islands. The Tahitian appellation is "Fehi" or "Fei," and this reappears in Samoa in the form of "Fa'i," the word for the common cultivated banana, Musa paradisiaca. The Rarotongan name of "Uatu," as given by Cheeseman, is suggestive of the Micronesian form (Ut, Uut, &c., in the Carolines) of a widely spread banana word in Malaya, Melanesia, and West Polynesia (Fudi, Vundi, Undi, &c., &c.). It is not unlikely that all these South Pacific mountain bananas with erect inflorescences and seeded fruits belong to one species, variously designated by botanists as Musa fehi, M. uranoscopus, M. troglodytarum, &c., and confined to this region. Under the name of Musa fehi Schumann includes the New Caledonian and Tahitian plants, and he views the Samoan plant as probably identical with them. This botanist, in his monograph on the Musaceæ (Engler's *Das Pflanzenreich*, 1900), establishes the home of the bananas in tropical Asia, and considers that their occurrence in America before the time of Columbus has not been proved. Birds have no doubt often assisted in the dispersal of the wild, seeded plants; but it is likely that man is responsible for the occurrence of the mountain forms in the Pacific, and probably their fruits formed when cooked one of the principal articles of diet of the earliest immigrants. (There evidently exists in Vanua Levu a plant very like the African Musa Ensete. Its presence was only indicated by the occurrence of its empty seeds in the stranded beach-drift, and reference is made to it in that connection in Chapter XXIX.)

(b) *The Polynesian food-plants.*—The cultivation of the yams,

the taros, the breadfruits, and the bananas in later ages all over the Pacific islands cannot here be dealt with. My readers will already know that a very ancient cultivation is in each case indicated by the occurrence of a great number of varieties. Much has been written upon this matter, and amongst the recent contributions to the subject may be reckoned Mr. Cheeseman's interesting paper published in the *Transactions and Proceedings of the New Zealand Institute* (vol. xxxiii).

I may here mention in connection with the Sweet Potato (Batatas edulis), a plant that may have an American origin, though much mystery surrounds its home, that it rarely seeds in Fiji except when it is grown in poor, sandy soil, and in dry, rocky situations. The Fijians were quite incredulous as to its maturing seed; but after much searching I found a solitary plant in seed and removed their doubts.

The Polynesian Weeds

Some curious questions are raised in connection with the weeds of this region. Polynesia, says Dr. Seemann, presents a most interesting problem with regard to its weeds. It is, however, necessary to point out that these plants arrange themselves into two groups, the aboriginal weeds comprising those existing in the islands at the time of Captain Cook's expeditions in the latter half of the eighteenth century, and the white man's weeds that have been since introduced.

As concerning the Fijian Islands, Dr. Seemann remarked that although the majority of the non-endemic plants of the flora is Asiatic, "the bulk of the weeds is of American origin, or, at all events, is now found in America." His principal point was to show that American weeds displayed a greater disposition than Asiatic weeds to spread in Fiji, because Fiji was to American plants altogether virgin ground. This is a purely botanical matter, and we are not in a position to oppose a conclusion formed by such a careful observer of plant life. But to the ethnologist it is a very different matter whether most of the Fijian weeds are of American origin or merely now exist in America. His interest lies entirely in the aboriginal weeds. To the student of plant-dispersal this distinction is also a very important one; and his interest again is all on the side of the aboriginal weeds.

Dr. Seemann enumerates 64 Fijian weeds, of which at least 37 were in the Pacific islands when Captain Cook's botanists made

their collections (see Note 82). Of these 22 occur in continental regions on both sides of the Pacific, 13 are natives of the Old World alone, and two only are seemingly American exclusively, namely, Waltheria americana and Teucrium inflatum. The first is claimed to be American because most species of the genus are American, but it is now widely distributed in the Old World as well as in America. The second, though widely distributed in tropical America, has strangely enough only been found in the islands of the Western Pacific.

The important point is thus brought out that although in Captain Cook's time the food-plants cultivated by the Polynesians, such as the banana, the breadfruit, the taro, and the yams, were almost exclusively Asiatic in origin and bore Malayan names, a large proportion of the weeds were not exclusively Asiatic, but occurred in America as well as in the Old World. The inference to be drawn, however, is not, as Dr. Seemann implies, that the Polynesians derived several of their weeds from America (since with few exceptions all the aboriginal weeds named in Note 82 occur in the Old World, and in more than a third of the plants in the Old World only), but that many so-called cosmopolitan weeds were distributed very much as they are now, when the Polynesians brought their food plants from Indo-Malaya into the Pacific.

Weeds follow the cultivator in all climates ; and it is very natural that, as Mr. Hemsley points out, plants which seem to owe their wide dispersal to cultivation are not found in Australia (*Bot. Chall. Exped.*, iii, 142). The Australian native as a rule cultivates nothing. Yet I fancy that man's share in weed dispersal is as often as not merely restricted to producing the conditions favourable to the growth of weeds, and that the seeds are often brought by birds and other agencies. Many weeds of the genera Atriplex, Polygonum, and Ranunculus are dispersed by partridges in England, and I have often found the uninjured fruits of the plants in the stomachs of these birds. Many weeds, like Prunella vulgaris, Plantago major, Capsella bursa-pastoris, Luzula campestris, and several others named in Note 43, possess seeds or fruits that become "sticky" when wet, and would readily adhere to a bird's plumage.

We can also say of tropical weeds that many of them are distributed by birds. In the crop of a dove in Hawaii I found a number of the small dry fruits of Waltheria americana, the widely spread tropical weed before mentioned, and of another weed of the order Compositæ. On the bare rocky peak of one of the Vanua Levu mountains the only plants found growing were Oxalis corni-

culata and a species of Peperomia, both of them evidently growing from seed dropped by birds. The fruits of Urena lobata and of species of Sida, as well as those of Bidens pilosa and Ageratum conyzoides, could be readily dispersed, entangled by their appendages in the plumage of birds, whilst the sticky achenes of Adenostemma viscosum would easily adhere to feathers. Weeds with drupes or berries like Geophila reniformis and Solanum oleraceum would attract frugivorous birds, and I have often seen berries of the last-named pecked by birds. Man has doubtless often been the agent in dispersing the seeds of Leguminous weeds like Lablab vulgaris. On the other hand, we know from the observations of Focke (see page 150) that birds can distribute the seeds of a plant like Vicia faba; and in the Pacific islands it is evident from the frequent occurrence of Tephrosia piscatoria on bare rocky hill tops that its seeds are dispersed through the same agency. Birds also probably carry about the seeds of Cardiospermum halicacabum.

If we based our conclusion solely on the distribution of weeds without a previous study of their means of dispersal we might, as students of the distribution of man, acquire some startling and very erroneous notions on the history of the races of man, especially in the New World. Lacking such an acquaintance with existing modes of dispersal it would not be prudent to attach too much importance to the occurrence of Asiatic weeds in America and of American weeds in Asia. Mr. Hemsley, in his work on the botany of Central America (*Biologia Centrali-Americana*), gives a list of ten British plants of world-wide range, which we will designate plants of waste places rather than weeds. They are plants often found not only in the Old and New Worlds, but also in the southern hemisphere, and I will here name them: Radiola millegrana, Alchemilla vulgaris, Cotyledon umbilicus, Lythrum salicaria, Convolvulus sepium, Sibthorpia europæa, Prunella vulgaris, Lycopus europæus, Aira cæspitosa, Luzula campestris. According to this authority these plants "are most unlikely to have been aided, intentionally or unintentionally, by man" and "possess no special means of dispersion by animals or birds or the elements" in the way, as is implied, of appendages like hooks, hairs, a pappus, &c.

Five of these plants are referred to in various connections already in this work. In all I have tested the means of dispersal of six or seven of them; and although my results are not always conclusive, I venture here to indicate some of them. The nutlets of Prunella vulgaris and the seeds of Luzula campestris emit mucus when wetted and adhere firmly to feathers on drying,

whilst the nutlets of Lycopus europæus are sticky in the dry state and adhere to the fingers on handling. This last-named plant is occasionally to be noticed on rubbish heaps growing with other waste-plants. No such adhesive qualities, whether in the wet or dry condition, came under my notice with Alchemilla arvensis or with Lythrum salicaria. With Alchemilla the seed-like fruits fall from the plant, inclosed in the dried-up calyx. The seeds of Cotyledon umbilicus are so minute ($\frac{1}{3}$ mm. or $\frac{1}{75}$ inch) that they can be compared with Juncus seeds from the standpoint of dispersal. They are naturally a little sticky and tend to adhere to feathers, but more probably they are transported in adherent soil. The case of Convolvulus sepium is a very remarkable one, and I have referred to it on page 29 and in the notes there indicated. The species of Radiola, Sibthorpia, and Aira have not been tested by me. Dispersion, however, would be favoured by the small size of the seeds in the first two species and by the awned glumes in the case of Aira.

The distribution of aboriginal weeds might be expected by some to supply data of profound interest to the student of the races of mankind ; and I think the botanist rarely realises how often he tantalises the ethnologist by the remark that certain weeds have been spread by cultivation all round the tropics. De Candolle many years ago, in his *Géographie Botanique*, gave a list of nearly 100 plants, made up of Old World species naturalised in America and of American species naturalised in the Old World, and quite half of them were classed as plants distributed in one way or another through man's agency. Now this is either a subject of supreme importance or it is of no interest to the student of man's history. If it should prove that birds have done most of this dispersal, then the story of the aboriginal weed would be of little interest in connection with the races of man in the New World.

I will now refer briefly from the standpoint of dispersal to a few interesting Polynesian plants in which man has been in most cases more or less concerned in their distribution.

Aleurites Moluccana (The Candle-Nut Tree)

Much interest is attached to this tree, which is found in India, Malaya, and North-east Australia, and occurs all over the Pacific, extending north to Hawaii, south to the Kermadec Islands, and east to Tahiti and Pitcairn Island (Maiden). In the Hawaiian Islands it is often so frequent as to form whole forests, or at all

events to give a character to the forest zone up to 2,000 feet above the sea. Its prevalence in Hawaii might be regarded as evidence of its indigenous character; but its predominance there is due to the circumstance that it is one of the few forest-trees that the cattle and other animals avoid, most other trees falling victim to their depredations by the loss of the bark. In Fiji, though frequent in places, it does not form such a conspicuous feature in the vegetation as in Hawaii. In Samoa it is abundant in the coast-bush. In Rarotonga it forms with Hibiscus tiliaceus, as we learn from Cheeseman, the major portion of the lower forests, a circumstance which seems to indicate, since both these trees were probably introduced by the natives, that this island like Hawaii has lost or is losing many of its original forest-trees. In Tahiti, according to Nadeaud, it is common from the sea-level up to 3,000 feet above the sea.

As a Polynesian tree, Aleurites moluccana presents itself to me as an intruder which has often taken the place of trees of the primeval forests of these islands. That the natives usually employ the oily seeds for illuminating purposes is well known; and its prevailing name of Tuitui (Kukui in Hawaii) is derived from the Polynesian custom of threading the seeds before using them for lighting purposes. One of the Fijian names, "Sikethi," is suggestive of "Saketa," a name for the tree in the Ternate dialect of the Indian Archipelago. To the modes of dispersal of this tree, I have devoted much attention.

The more or less empty seeds of this tree are to be commonly found floating in rivers and stranded on beaches. I have found them in numbers on the beaches of Fiji and Hawaii in the Pacific, and of the south coast of Java and of Keeling Atoll in the Indian Ocean. In all I have examined many hundreds of these seeds, whether stranded on the beaches in the localities above named, or floating in the Fijian rivers and at sea amongst the islands of that archipelago. The seeds were always either empty or contained a kernel in an advanced stage of decay. A sound seed has no floating power under any condition; and sound seeds are only to be found in beach drift near the mouths of estuaries, where they have been freed by the decay of the fruits brought down by the rivers. During some dredging operations in the harbour at Honolulu several years ago, quantities of old Aleurites fruits and seeds were brought up. It is only by means of the floating fruit that the sound seed can be carried any distance by the currents; but even in this case the opportunities of wide

dispersal are very limited. If one places in sea-water a number of well-dried fruits, most of them will sink within a week, and all will be at the bottom in a fortnight.

The seeds stranded on a beach are often found cracked. This I think arises from long exposure to the scorching rays of the sun. On account of the hardness of the shell it is very difficult to obtain the kernel entire; but the Mangaians get over this difficulty, as we learn from the Rev. Wyatt Gill, by slightly baking the seeds; whilst the Fijians, according to Mr. Horne, effect the same object by throwing the heated seeds into cold water. On one occasion I placed an empty seed on a tin plate kept at a temperature 115° to 120° F., a temperature near that which the seed would acquire when lying exposed to the sun on a tropical beach. After five days I found it had reproduced the cracks noticed in another empty seed from the Keeling beach.

Facts are not wanting with regard to the dispersal of the seeds by birds; but since the kernel alone is sought for by birds, and as there is no means of cracking the shell in their stomachs, such an agency is only available for local distribution. The Messrs. Layard inform us that in New Caledonia a small crow (Physocorax moneduloides) and a parrot (Nymphicus cornutus) are very partial to these seeds (*Ibis*, 1882). They were told that the crow cracked them by carrying them to a considerable height and letting them fall on a stone. We are not told how the parrot cracks the seed, which has a shell so hard that the Malays, I may remark, term the seed "bua kras," or "the hard seed," whilst a hammer is required to break it. However, since Indian parrots, according to Mr. J. Scott, are able to split open with their beaks the hard beans of Adenanthera pavonina (*More Letters of Charles Darwin*, ii, 349), they evidently possess ingenuity in seed-cracking.

My general conclusion with reference to this tree in Polynesia is that it could not have been distributed, except locally, by birds and currents; and that it owes its dispersion there principally to man. A contrary indication seems to be offered by the occurrence of the tree in the uninhabited Kermadec group; but since Cordyline terminalis also exists there, a cultivated plant widely dispersed by the Polynesians, it would appear that these islanders have formerly visited the group. It is also contended by Canon Walsh that the Cordyline of the Maoris was introduced into New Zealand by that race. (See Cheeseman in vols. xx and xxxiii, *Trans. N.Z. Inst.*, for papers on the Kermadec flora and on the food-plants of the Polynesians.)

INOCARPUS EDULIS (THE TAHITIAN CHESTNUT)

Like Aleurites moluccana this tree presents a *primâ facie* case for dispersal by currents. As the result of inquiries in this direction I have formed the opinion, however, that it has been mainly distributed by man. Though occurring in all the South Pacific groups, as far east as Tahiti and the Marquesas, it does not occur in Hawaii. With its home in Malaya it possesses a range closely resembling that of the breadfruit tree; and yet, although its fruits are often a common article of food in Polynesia, it requires no cultivation, and reproduces itself so abundantly in favourable situations that, as Dr. Seemann observes, only the dense shade of the parents checks the occupation by the seedlings of all the adjacent ground. It possesses in the Pacific two sets of names, neither of which I have been able to identify with any Malayan names, and both occur over much of the region. Thus the Fijian "Ivi" and the Samoan and Tongan "Ifi" are represented by "Ii" in Rarotonga, "Ihi" in Tahiti and the Marquesas, "Hi" in Ualan in the Carolines, "Ifi" in Futuna in the New Hebrides, and "If" in a New Guinea dialect. Then we have the Tahitian "Mape," the "Marap" of Ponape in the Carolines, and the "Mamape" of Fate in the New Hebrides, besides other forms found in Melanesia.

In the South Pacific islands, as in Fiji, Samoa, Rarotonga, and in the Tahitian group, it flourishes in low, moist localities at and near the coast, by the side of streams and estuaries, and in the rich soil of the lower valleys. In the Rewa delta in Fiji it is especially abundant, often bordering the creeks in the mangrove swamps, and occupying stations that are under water when the river is in flood. It may extend inland in the various groups, but it is in the low-lying, moist, coast regions that it mostly thrives; and in Fiji it presented itself to me as essentially a tree of the estuaries, a station strongly suggestive of dispersal by currents. Schimper, it may be remarked, includes it amongst the shore vegetation of the Indian Archipelago.

When in Fiji I paid especial attention to the dispersal by currents of these large fruits, the agency of birds being, of course, negatived by their size. They are to be commonly observed floating in the rivers when in flood, as well as at sea between the islands, and stranded on the beaches. Of those found afloat in the Rewa River not more than a fourth had a sound seed. Of those

stranded on the beaches two-fifths were empty, two-fifths displayed a rotten seed, and one-fifth had sound seeds. Of those picked up at sea all were empty. These fruits, unlike many others in the drift of the Fijian rivers, do not germinate afloat. They soon lose in the water their outer, fleshy, non-buoyant coat; whilst the inner fibrous coat, to which the floating power of the fruit is due, the seed having no buoyancy, is not water-tight, and moisture soon enters and leads to the decay of the seed. In order to test their floating power, I placed in sea-water ten mature fruits. Five of them floated after forty-five days, having then lost most of the outer, fleshy coat. Two were afloat after sixty days, but their seeds were rotting. One fruit that sank after five weeks had a sound seed. Most of them were sown out afterwards in a place where the trees were thriving, but none germinated, and of two or three examined all had a decaying seed. The empty fruits may float a long time after the decay of the seed. Forty days would probably be the extreme limit for the flotation in sea-water of a fruit with a seemingly sound seed, though a very small proportion would reach this limit, and I much doubt whether such a fruit would germinate afterwards.

I, therefore, inferred that currents are only available for the local dispersion of the fruits of Inocarpus edulis. It is to man that the tree owes its existence in Tahiti and other groups of the open Pacific; and it is to be concluded that the occurrence of this tree on Christmas Island in the Indian Ocean marks an early Malayan occupation of the island.

Gyrocarpus Jacquini

The cosmopolitan distribution of this seemingly useless tree, growing, as Hemsley remarks, in maritime districts throughout the tropics, in America, Australia, Asia, and Africa, presents one of the puzzles of plant-distribution. It is by no means universally spread in the Pacific islands, and I find reference to it only in Fiji and Tahiti. Seemann says that in Fiji it is common on the beaches of Taviuni and other islands. I found it to be a rare coast tree on Vanua Levu. It does not seem to have been recorded by the botanists of the 18th century in the Pacific. It, however, has evidently been long established there. Nadeaud does not speak of its littoral station in Tahiti, and says that it grows best in the regions of the interior up to elevations of 2,000 feet, where it

attains a great size; and its abundance is implied by his remark that he had to fell many trees to collect the fruits.

The singular fruit, which has two long wings and looks like a shuttlecock, dries up on the tree; and in course of time it is detached and falls to the ground. The falling fruit in its descent twists round like a screw, and hence the Fijians call the tree the Wiri-Wiri tree, the same name in the form of Wili-Wili being given for a similar reason to Erythrina monosperma in Hawaii. Schimper (p. 157) truly remarks that the fruits are too heavy to be carried by the wind across a wide extent of sea; and I ascertained by experiment that in an ordinary trade-breeze they would only be carried a few paces. Birds are quite out of the question as agents of their transport to oceanic islands. We are driven then either to the agency of man or to that of the current. The trees grow rapidly and the timber is soft and perishable. The fruits are not edible, and as far as I could ascertain the tree is of little or no value to the Pacific Islander, there being at all events no reason to believe that he has distributed it.

We appeal lastly to the currents, the agency which Mr. Bentham selected on *a priori* grounds (Presidential address, *Linnean Society*, 1869). My experiments in Fiji showed that the fruits, when dried on the tree and afterwards detached, are able to float over long distances in sea-water. After two months they were still afloat, the seeds inside being dry and unharmed. The fruit's buoyancy was tested in different conditions, either without the wings, or with both wings, or with but one wing, and it was found that the wings, which float for only a day or two by themselves, lessen the buoyancy of the fruit. Of fruits with both wings attached forty per cent. floated after two months, whilst of those deprived of the wings all floated after two months. In the ordinary course of flotation the wings in most cases break off during the first few weeks, and in the rough-and-tumble of current-transport this would occur sooner, so that the floating power of most of the fruits would not be much affected. The cause of the buoyancy in a structural sense belongs to the Convolvulaceous type. The kernel has no buoyancy, but it incompletely fills the cavity of the seed-vessel, the coats of which are quite waterproof, but have no independent floating power.

It is thus evident that like many other shore-trees Gyrocarpus Jacquini is distributed by the currents. It is not unlikely that its present sporadic occurrence in the Pacific islands may be due to the gradual extinction of the tree in this region, either on account

of some insect pest introduced since Cook's time or from the use of the timber for fire-wood by the aborigines.

SERIANTHES MYRIADENIA

This is a striking looking Acacia-like tree that might have been fitly discussed in the chapter on the enigmas of the Leguminosæ. Only four or five species are named in the *Index Kewensis*, of which one occurs in Malacca and in the Philippines, a second in New Caledonia, a third in Fiji, and the fourth, S. myriadenia, over the South Pacific groups of Fiji, Tonga, and Tahiti. Reinecke does not include the genus in the Samoan flora; and it is merely assigned to that group by Seemann on the authority of Mr. Pritchard, the British Consul in Fiji. Though common in the forests of the larger islands of Fiji, S. myriadenia is most at home on the banks of the estuaries, usually behind the mangrove belt, but not beyond tidal influence. The peculiar species, S. vitiensis, I found on the banks of the estuary of the Mbua River in Vanua Levu, the locality from which Gray described it. According to the French botanists, S. myriadenia, in Tahiti, ranges from near the sea to an elevation of 800 metres. The Fijian name of the trees is "Vaivai," the name also of Leucæna Forsteri, and of some other introduced trees of the Acacia habit. The Tahitians apply the same name in the form of "Faifai" to S. myriadenia.

The Fijians value the trees on account of the wood; but unless the Polynesians were in the habit of transporting the seeds of their numerous timber trees, which is most unlikely, it seems at first sight useless to look to man's agency for an explanation of the wide dispersal of a tree like S. myriadenia in the South Pacific. The tough, woody, indehiscent pods, from 3½ to 4 inches long, floated in my sea-water experiments in the case of both S. myriadenia and S. vitiensis between seven and twenty-five days, after drying for some months. The seeds, about two-thirds of an inch (17 mm.) in length, are only freed by the decay of the fallen pod, and have no buoyancy. The agency of birds is evidently excluded; and it is, therefore, to the currents that we must make our final appeal; but their powers of dispersing the species appear quite insufficient to explain the occurrence of these trees in Tahiti. Perhaps, as in the case of Calophyllum spectabile, another Polynesian timber-tree found in Tahiti (see p. 136), man and the currents have worked together.

Leucæna Forsteri

This bush of the Mimoseæ frequents maritime sands in the South Pacific, and is confined to this region. It has been found in New Caledonia, Fiji, Tonga, Rarotonga, and Tahiti. The seeds sink and the pods dehisce on the plant, so that the agency of currents, unless we invoke the intervention of the drifting log, bearing the seeds in its crevices, seems to be excluded. Sea-birds might carry the seeds unharmed in their stomachs, but there is no evidence bearing on birds as agents in the dispersal of the species. Since the plant has not been recorded from localities outside the Pacific islands, and since it was collected by Cook's botanists in Tonga and Tahiti, it cannot be placed amongst plants of recent introduction. Although growing on maritime sands in Fiji, Rarotonga, and Tahiti, it may grow inland, and according to Cheeseman is particularly abundant in Rarotonga. In Fiji it is apt to occupy newly-formed alluvial land at the mouth of the rivers, as in the case of the Rewa; but the "how and why" caused me much fruitless speculation, and I abandoned the plant in despair. The Fijians sometimes give it the native name of Serianthes myriadenia, which they then term "Vaivai ni Viti," or the Fijian Vaivai. In Tahiti it is named "Toroire," and in Tonga "Toromiro."

Mussænda frondosa

Mussænda frondosa is the only one of the sixty species of this tropical Asiatic and African genus that extends into Polynesia. This beautiful shrub, which is easily recognised by its conspicuous white, leaf-like calyx lobe, is common everywhere in Fiji, decorating, as Horne fitly remarks, in the contrast presented by its golden flowers, its large white calyx leaf, and its green foliage, many an acre of waste, grassy land, where the orange-coloured doves and the red and the green parrots flit to and fro. With its home in India, China, and Malaya, it ranges all over the South Pacific, from the Solomon Islands to Tahiti. Its berries contain an abundance of small, minutely-pitted seeds, 0·7 mm. or $\frac{1}{35}$ of an inch in size, and weighing when well dried about 600 to the grain. The seeds retain after years of drying the property of clinging to passing objects by means of a few microscopic, thread-like fibres, that are attached to their surfaces. In this manner they will fasten themselves to the point of a knife, and the observer is astonished to see them

dangling in the air from a pin's point. I suppose that this is connected with some hygroscopic quality. At all events, it would enable these light seeds to be carried about not only by birds and bats but also by insects. It is possible that man has aided in the dispersal of this interesting plant; but birds, bats, and insects have, I think, mainly done the work.

LUFFA INSULARUM

This is regarded as a maritime form of Luffa cylindrica, a plant commonly cultivated throughout the tropics. The South Pacific plant, which occurs also in Australia and Malaya, has been found in New Caledonia, Fiji, Tonga, Rarotonga, and Tahiti. In Fiji it grows chiefly on the "talasinga" plains and in places once under cultivation. I noticed it in one locality climbing over the branches of an Inocarpus tree on the banks of the Rewa. In Rarotonga it is common in the lower regions. It is, according to Nadeaud, fairly frequent on the shore and in the lower valleys of Tahiti, where it was collected by Banks and Solander, the companions of Cook. The Pacific islanders, as far as can be gathered, make little or no use of the plant; and unless it was introduced accidentally with their cultivated plants, they could scarcely have been concerned in its dispersal.

In Fiji I made a special point of investigating the mode of dispersal of this plant. The fruits, which ultimately become dry and fibrous, are to be seen hanging vertically from the plant as it climbs among the branches of a tree. The apical disk usually falls off, and many of the seeds drop out through the hole thus produced; but a few remain entangled in the fibrous material occupying the interior of the fruit. I have noticed such fruits floating down the stream of the Rewa River; but my experiments showed that they do not float more than a week, whether in fresh or salt water. The seeds, however, possess a hard, impervious shell, and are well adapted to withstand unharmed prolonged immersion in the sea. They will evidently float for months. Out of one hundred selected seeds placed in sea-water, sixty were found afloat and sound after two months. The cause of the seed-buoyancy is purely mechanical. Neither the shell nor the kernel has any floating power, the buoyancy arising, as with Convolvulaceous seeds, from the unfilled space in the seed-cavity. When in Fiji, I tested the seeds of the ordinary cultivated tropical form of the plant which had been

introduced into a garden from Australia. They all sank in a few days, and on being cut across the seed displayed but little unoccupied space in its cavity. I have no doubt that the Pacific form of this plant has been at times dispersed by the currents, not, however, through the fruits, but through the seeds. It is also quite possible that it may have been introduced by a pre-Polynesian people into the Pacific.

Summary of the Chapter

(1) Man in his distribution over the Pacific islands reproduces, but in a less degree, nearly all the difficulties presented by the plant in its dispersal. In both we have the age of general dispersion followed by a suspension more or less complete of the migrating movements; and in both we have differentiation associated with the isolation.

(2) The Pacific islanders possess two sets of food-plants. In addition to those commonly cultivated in our own time, such as the yam, the taro, the banana, &c., there are a number of food-plants now growing wild, but rarely cultivated, and only used when the others fail. These plants, which include the wild yams, the mountain bananas, Tacca pinnatifida, Pandanus odoratissimus, and several others, are regarded as older than the Polynesians in the Pacific, and as having probably formed the food of a pre-Polynesian race that practised only a rude sort of cultivation.

(3) The weeds of Polynesia also fall into two groups. In the first place there are the aboriginal weeds, of which those found in this region by Captain Cook's botanists in the latter part of the 18th century are taken as examples. These include species of Urena and Sida, besides Waltheria americana, Oxalis corniculata, Bidens pilosa, and many other weeds. In the second place, there are the numerous weeds that are known to have been introduced by the white man since the voyages of the English and French navigators of Captain Cook's time.

(4) There is reason to believe that many weeds now cosmopolitan in the tropics had obtained their present distribution in America and in the Old World before the Polynesians entered the Pacific. It is thus that we can explain how there existed in these islands at the time of their discovery by Cook, Bougainville, and other navigators of that period, a number of weeds that have their homes in America.

(5) It is not considered that the distribution of aboriginal weeds can materially aid the ethnologist in his study of the early history of man, since birds are regarded as the chief distributors of their seeds and fruits. Whilst man has prepared the conditions for the growth of weeds, the bird has usually brought the seeds.

(6) Amongst interesting plants concerned with man in the Pacific are Aleurites moluccana and Inocarpus edulis, which are regarded as in the main distributed through man's agency. Gyrocarpus Jacquini is viewed as a tree originally widely dispersed by the currents in the Pacific, but now becoming extinct.

CHAPTER XXIX

BEACH AND RIVER DRIFT

In the south of England.—On the coast of Scandinavia.—In the Mediterranean. —Southern Chile.—Very little effective dispersal by currents in temperate latitudes.—Cakile maritima.—In tropical regions.—River drift.—River and beach drift of Fiji.—Musa Ensete.—The coco-nut.—River and beach drift of Hawaii.—Comparison of the beach drift of the Old and New Worlds.—Summary.

THE BEACH DRIFT OF TEMPERATE LATITUDES

DISPERSAL by currents seems to be mainly restricted to warm latitudes. Whilst in the tropics seed-drift is abundant on the beaches, in the cooler regions of the globe it is usually very scanty and often masked by other vegetable *débris*.

Let us take, for instance, a beach in the south of England. We can find by careful searching amongst the stranded drift the seeds and seed-vessels of various littoral plants of the buoyant group, such as Arenaria (Honckeneya) peploides, Cakile maritima, Crithmum maritimum, Convolvulus soldanella, Euphorbia paralias, &c., and such sundries as bits of stems of Salsola kali bearing fruits; but their amount is scanty; and they are often difficult to find on account of the great amount of rubbish with which they are associated, such as empty stones of cherries, plums, and peaches; empty seeds of grapes; hazel-nuts, beech-nuts, chestnuts, acorns, all either empty or with decaying seed; the spiral pods of Medicago; besides quantities of leaves, sticks, and bark. Although the occasional shell of a Spirula, or the horny skeleton of a Velella, or a genuine pumice pebble (see Note 76), may tell us of long wanderings in mid-ocean, we find little that is not English or derived from neighbouring coasts on a beach in the south of England. I have examined numerous beaches on the coasts of

Devon and Cornwall, and have never come upon any indubitable tropical seed-drift.

On one occasion I examined many of the beaches between Ilfracombe and Padstow with the object of finding tropical seeds, but to no purpose. Portions of bark, generally 2 to 4 inches across and much water-worn, together with a quantity of steamer-slag or cinders, often largely composed the stranded drift. No doubt this bark is stripped off by the waves from floating trees, which are generally stranded in a bare condition after a long ocean voyage. This is the case with the timber brought in the Oregon drift to Hawaii; and Sernander (p. 117) remarks that bark seldom occurs on the trees washed ashore with the Atlantic drift on the coasts of Scandinavia. Modern marine deposits ought to contain much bark *débris*.

On the beaches in the vicinity of estuaries we find a certain amount of river drift, and amongst it fruits or seeds of Sparganium ramosum, Iris pseudacorus, Alnus glutinosa, Rumex, and many other river-side plants, such as I have mentioned in my paper on the Thames drift (*Journ. Linn. Soc. Bot.*, xxix). Most of them are capable of reproducing the plant, but not on the sandy beach where the waves have stranded them; and we thus see here one of the limits of the efficacy of currents as seed-dispersers.

From the labours of Lindman and Norman, the results of which are summed up by Sernander (p. 116) we can learn what are the components of the "Atlantic Drift" on the Scandinavian coast; and a strange assortment we here find, in which it is difficult to detect much indication of effective seed dispersal. Besides the seeds of Cæsalpinia Bonducella, Entada scandens, and Mucuna urens, familiar to us as occurring in the drift of tropical beaches, there is a quantity of vegetable drift hailing sometimes from North America, sometimes from the Canary Islands, and sometimes from the West Indies, mingled with much local drift in which the larch and steamer-slag or cinders predominate. The seed-drift derived from the proper beach-plants of the coast plays a subordinate part, though it is stated by Norman and others that seeds and seed-vessels, as the case may be, of Arenaria peploides, Cakile maritima, Convolvulus soldanella, and Lathyrus maritimus, with those of other plants, are also to be found.

The Mediterranean beach drift, as illustrated by the results of my examination of numerous beaches in Sicily as well as in the islands of Stromboli and Lipari, and of the beach at Cumæ, is of a scanty nature. If we eliminate the various evidences of cultiva-

tion which seem to occur over much of the temperate regions of the globe, very little remains of an interesting character. As in the south of England and in other regions, the empty stones of the cherry, plum, and peach, the empty nuts of the oak, hazel, &c., together with the spiral pods of Medicago figure largely in the drift; and here and there we come upon the seeds of littoral plants, such as Convolvulus soldanella and Euphorbia paralias.

I have found Medicago fruits in all these localities on the beaches. They often contain seeds, which, it may be added, have no buoyancy, the seeded pods themselves floating from two to five days. The pods of several kinds of Medicago form the great feature of Sicilian drift and are often indications in other places of the vicinity of cultivated districts. A small hairy species thrives on Letojanni beach near Taormina, and I observed its seeds together with those of Euphorbia paralias germinating in the drift stranded on the same beach. Arcangeli, in his *Flora Italiana*, enumerates as many as thirty-three species of Medicago. Many of the species grow in maritime districts, and their fruits must often get into the beach drift independently of cultivation. I noticed the pods amongst the drift brought down by the Alcantara, a river near Taormina, a fact which goes to explain their presence in beach drift. . . . On the beach of Trogilus Bay, near Syracuse, I gathered several fruits of a Vitex, apparently V. agnus castus. After being kept afloat for six weeks in sea-water some were placed in soil, when they soon germinated and reproduced the plant.

The beach drift of temperate Chile is described in Chapter XXXII. There, as in other beaches of cool latitudes, it is not easy to find seeds amongst the rubbish; but amongst the scanty seed-drift may be recognised much of what we are familiar with in the Old World, such as the seeds of Convolvulus soldanella, bits of the fruiting stems of Salsola kali, as well as the rubbish indicating the white man's presence, such as empty stones of cherry, plum, and peach, Medicago pods, &c. In addition, we find the seed-vessels of plants like Franseria and Nolana that are peculiar to American beaches; and now and then, the seeds of Sophora tetraptera, a tree of the immediately adjacent hill-slopes, come under our notice.

Before quitting this subject of the beach seed-drift of temperate latitudes, it may be observed that when at San Francisco I visited the beach running south from the Golden Gate. With the exception of the fruits of Cakile maritima, a plant growing on the beach, few other seeds or fruits were observed in the drift.

The inference that there is very little effective dispersal by

currents in temperate regions is of some importance, and Sernander arrived at a similar conclusion when discussing the origin of the Scandinavian flora. The few plants with buoyant seeds and fruits, such as Arenaria peploides, Cakile maritima, Crithmum maritimum, Convolvulus soldanella, Euphorbia paralias, and Lathyrus maritimus, are no doubt thus dispersed, and Norman is quite right in attaching some value to the distribution by currents of certain plants within the region of the Arctic flora ; but after all it amounts to little, and geographical and climatic conditions have often had a predominant influence in determining the distribution in the temperate latitudes of littoral plants possessing buoyant seeds or fruits.

Nowhere is this shown more plainly than with the littoral plants with buoyant seeds or seed-vessels that are found on our English beaches. Some have evidently acquired their present distribution before ice and snow reigned supreme in the extreme north. Though it may be possible, it seems highly improbable, that either Arenaria peploides or Lathyrus maritimus, both of which occur on beaches in high northern latitudes in the Atlantic and Pacific Oceans (as in Arctic Norway, Spitzbergen, and Behring's Straits), could possess in our own day any means of communication between their areas of distribution on the borders of these two ocean-basins.

So again with Cakile maritima, the occurrence of this or of two closely allied species on both sides of North America cannot be attributed to any present working of the currents for two reasons. In the first place, as is remarked in Note 18, the results of two independent experiments made by me show that the fruits will not float more than a week or ten days in the sea, a capacity that will not admit of their transportation by the currents over tracts of ocean more than one or two hundred miles across. In the second place, this species is not an Arctic plant like Arenaria peploides and Lathyrus maritimus ; and the possibility of inter-communication between the Atlantic and Pacific Oceans having any effective value from the standpoint of dispersal, shadowy as it is with the two Arctic species, is still more so in the case of Cakile maritima. Norman's observations on the coast of Norway, as quoted by Sernander (page 123), indirectly indicate how hopeless it would be for this plant to attempt to traverse the Arctic region. Just as I have noticed on the north coast of Devonshire, the fruits occur plentifully in the beach drift and germinate freely in the upcast wrack as far north as Senjen in latitude 69°. Further north the plant has been recorded from only eight localities, and since it is

there sterile and but a summer annual, the seed-vessels, it is argued, must have been brought by the currents from the south.

The reference to Cakile maritima as a summer annual on the north coast of Norway is of interest; but I may point out that it displays a similar behaviour in England on the north coast of Devonshire. Here, during the latter half of July, 1903, I found the fruits common in the stranded drift, and often in a germinating condition, whilst numerous seedlings one to two inches high with the fruit-shell still attached were growing out of the sand. From this arises the curious reflection that an annual which germinates in the end of July could scarcely be expected to mature its fruit before the winter. It would seem that this beach plant hampers its own dispersal by its misdirected efforts; and the idea suggests itself that we have here the explanation of its sterility in the north of Norway. Had it been a perennial like Arenaria peploides and Lathyrus maritimus it might have had a similar distribution within the Arctic Circle.

Quite other considerations seem to be suggested by the perennials Crithmum maritimum and Euphorbia paralias. In these cases, although the seeds or fruits, as the case may be, will float for months in sea-water without apparently sustaining any injury, the species are confined to the warmer parts of the European region.

From Convolvulus soldanella we obtain another story. Its occurrence in the temperate regions of both the northern and southern hemispheres, great as the floating powers of the seeds may be, is concerned with something more than with questions relating to modes of dispersal. The circumstance that in its distribution in the temperate regions it is practically coterminous with Ipomea pes capræ in the tropics is very significant (see Note 49).

Each one of the English beach plants with buoyant seeds and fruits has its own story of the past to tell. Time has indeed gathered on our beaches current-dispersed plants, which, if they could speak, would tell us strange stories of many latitudes, stories of change within the Arctic Circle, and stories of great events within the temperate regions, and, as in the case of Convolvulus soldanella, stories of a past within the tropical zone. It cannot be said that investigators lack clues leading to lines of inquiry into the age that immediately precedes our own.

Yet valuable as our British plants would be for this purpose, they do not afford any indication that currents have played an

important part in plant distribution in temperate and arctic latitudes. Ekstam strikes the true note for these regions when discounting the agency of currents in the instance of the Spitzbergen flora, he regards the wind as the greatest factor in seed-dispersal and after that the bird. The several interesting points raised by this botanist are discussed in Chapter XXXIII.

The Beach-Drift of Tropical Latitudes.

Tropical beaches, as a rule, present a much greater abundance and variety of stranded seeds and fruits than we find on beaches in temperate latitudes. Observers in different parts of the tropics have alluded to the enormous amount of vegetable drift floating in the sea off the coasts, particularly in the vicinity of estuaries. Though much of it is brought down by rivers, a good proportion is also derived from the luxuriant vegetation that lines the beaches. Gaudichaud speaks of the immeasurable quantity of drift (trees, branches, leaves, flowers, fruits, and seeds) floating amongst the islands of the Molucca Sea; and Hemsley, who quotes this author, gives other facts illustrating the same point. Moseley tells us that seventy miles off the coast of New Guinea, H.M.S. *Challenger* found the sea in places blocked with drift (*Bot. Chall. Exped.* iv. 279, 284). When the author of this book was in the Solomon Group, long lines of vegetable drift were frequently observed floating among the islands. The Rewa River in Fiji carries down a great amount of drift to the sea; and as described in Chapter XXXII, the Guayaquil River in Ecuador bears seaward an enormous quantity of these materials.

When we come upon this floating drift out at sea off an estuary, we find, as Mr. Moseley pointed out, that the leaves have gone to the bottom, whilst the floating islets, composed of the matted vegetation lifted up from the shallows of a river channel, which form such a feature in the Guayaquil River, have been dispersed or sent to the bottom. However, a very large proportion of the seed-drift brought down by a river from the interior has no effective value for the purposes of dispersal. Many of the fruits and seeds brought down from inland owe their presence in river-drift entirely to the buoyancy acquired by the decay of the seeds. It is in its lower course when it traverses the mangrove belt that a river picks up most of the material that is of service in distributing the species; and this is mingled out at sea with the numerous buoyant

seeds and fruits of littoral plants that are swept off the beaches by the currents.

A description is given in Chapter XXXII of the enormous amount of vegetable drift brought down by the Guayaquil River to the coast of Ecuador. Besides the huge tree-trunks and the floating Pistias, we observe large islets formed mainly of Pontederias and Polygonum, together with a host of seeds and seed-vessels, both large and small, including those of Anona paludosa, Entada scandens, Erythrina, Hibiscus tiliaceus, Ipomea, Mucuna, Vigna, &c., accompanied by the empty seeds of Phytelephas macrocarpa and of many other strange plants from the slopes of the Chimborazo mountains. In addition, we notice the seedlings of Avicennia and of Rhizophora mangle together with the seeded joints of Salicornia peruviana and the germinating fruits of Laguncularia.

When in Fiji I made an especial study of the drift of the Rewa Estuary within tidal influence, the results of which are incorporated in various parts of this work. In the rainy season, when the drift is most abundant, the following would be its most characteristic components:

Seedlings of Bruguiera and Rhizophora.

Fruits of Barringtonia racemosa and B. speciosa, the first-named most abundant and often germinating.

Seeds of Carapa obovata, most of them far advanced in germination.

Fruits of Lumnitzera coccinea.

Fruits of Cerbera odollam, abundant.

Fruits of Inocarpus edulis, with the seed generally rotten.

Fruits of Heritiera littoralis, Parinarium laurinum, and Pandanus.

Empty seeds of Aleurites moluccana.

Fruits of Scirpodendron costatum, abundant.

Fruits of Clerodendron inerme and Smythea pacifica, both of them in some cases germinating.

Pyrenes of Morinda citrifolia.

Small fruits of Vitex trifolia and Premna taitensis, both sometimes abundant.

Seeds of Entada scandens, Mucuna, and Vigna lutea.

Pods of Dalbergia monosperma and Derris uliginosa, the last sometimes in a germinating condition.

Seeds of Hibiscus tiliaceus and of different species of Ipomea, such as I. peltata and I. pes capræ.

Amongst other seeds and fruits brought down by the Fijian rivers and stranded with a large amount of miscellaneous vegetable *débris* on the beaches in the vicinity of the estuaries are the seeds of Dioclea, Strongylodon lucidum, and Afzelia bijuga; the empty seeds of Musa Ensete (as identified with a query at Kew); the empty stones of the Sea tree, apparently a species of Spondias; the seeds of Colubrina asiatica; the fruits of an inedible indigenous Orange (Citrus vulgaris ?) referred to in Chapter XIII; the cocci of Excæcaria Agallocha and Macaranga; and Coco-nuts.

The occurrence in Fijian beach-drift of the seeds of Musa Ensete, or of a wild banana much like it, is very remarkable. This species is found in the mountains of Abyssinia and on the slopes of Kilima-njaro in Equatorial Africa; but according to the monograph by Schumann on the Musaceæ (Engler's *Pflanzenreich*, 1900) the species is confined to Africa, whilst all the other species of the subgenus are mostly restricted to the same continent with the exception of one or two in Further India. The empty seeds are frequent on the beach at Duniua at the mouth of the Ndreke-ni-wai in Savu-savu Bay, Vanua Levu, and are doubtless brought down by that river. Strangely enough the natives could give me no information about the parent plant which I never discovered. The seeds did not come under my notice in any other locality in Fiji. They answer to the description and to the figure given by Schumann for Musa Ensete; and their presence in the drift is one of the mysteries of the Pacific floras.

To enumerate the seeds and fruits found stranded on beaches in Fiji would be to give a list of all the littoral plants with buoyant seeds or fruits that are included in the list given in Note 2. I may here allude to the fact that the Coco-nut, whether brought down by a river or transported by a current, is able to germinate and establish itself when washed up on the Fijian beaches. I have found these fruits germinating amongst the drift stranded on the beaches near the mouths of rivers, some just beginning to germinate and others already striking into the sand and showing the first leaves. White residents living for years in one locality were quite convinced that this frequently happens. One of them pointed out to me some newly formed land at a river's mouth, not over two years old, on which were growing young plants three or four feet high of Barringtonia speciosa, Calophyllum Inophyllum, and several other plants including young Coco-nut palms, all growing from fruits washed up by the waves and therefore self-sown.

Like the littoral flora the beach-drift proper to the Hawaiian

Islands is very scanty. This is due to the scarcity of rivers, to the absence of the mangrove-formation from which much of the drift is derived in other tropical regions, and to the paucity of shore-plants with buoyant seeds or fruits. As is observed in Note 30, where the composition of the beach drift is described, the presence of a large amount of timber and of other materials brought by the currents from the north-west coast of America masks much of the local drift.

Remarks on the beach-drift of the Panama Isthmus, and of the Ecuadorian, Peruvian, and Chilian coasts of South America will be found in Chapter XXXII. I have examined beach drift in other tropical regions, as in the Solomon group, on Keeling Atoll, and on the south coast of West Java ; whilst there are at my disposal the data supplied by Schimper and Penzig for the Malayan region including Krakatoa, and by Hemsley for tropical regions generally. It will, I think, be best, if instead of describing in detail the composition of the drift for each locality, I refer briefly to the features that distinguish the tropical beach-drift of the Old World from that of the New World.

The beach-drift reflects the characters of the coast flora ; and since tropical littoral floras belong to two great regions, the Asiatic including Polynesia and the African East Coast, and the American including the African West Coast, the seeds and fruits stranded on the beaches may be similarly referred to the same two regions.

All over tropical Asia, as well as in the tropical islands of the Indian and Pacific Oceans, the drift stranded on the beach presents the same general character, and as a rule possesses seeds and fruits of the same species that range over the whole or the greater part of this region. Almost everywhere we find seeds or fruits of the same plants of the beach formation, such as Barringtonia speciosa, Cæsalpinia Bonducella, Calophyllum Inophyllum, Canavalia obtusifolia, Cerbera Odollam, Cordia subcordata, Entada scandens, Guettarda speciosa, Hernandia peltata, Hibiscus tiliaceus, Ipomea pes capræ, Mucuna, Scævola Kœnigii, Sophora tomentosa, Terminalia Katappa, and Tournefortia argentea. In those localities where mangrove-swamps occur we find generally diffused in the stranded drift of this region the seedlings of Bruguiera and Rhizophora, the seeds of Carapa moluccensis, the fruits of Heritiera littoralis and Lumnitzera coccinea, and the pods of Derris uliginosa. Amongst sundries found over much of this region may be mentioned, the drupes of Pandanus, the seeds of Erythrina, Vigna lutea, and Hibiscus tiliaceus, and the "nuts" of

Aleurites moluccana. With the exception of the last-named all the fruits and seeds here enumerated are effectively dispersed by currents over great areas. The sound nuts of Aleurites have no buoyancy; and the nuts only acquire their floating power through the decay of the kernel (see p. 419).

The beach drift of the American region, a region which comprises both the Pacific and Atlantic coasts of tropical America as well as the African West Coast, has some features in common with the Asiatic beach-drift and other features peculiar to itself. The plants, however, that are represented in the drift of both regions are comparatively few, and none of the large fruits of the Asiatic region are here to be noticed. We observe, however, that the drift of the two regions possess in common the seeds of Cæsalpinia Bonducella, Canavalia obtusifolia, Entada scandens, Erythrina, Mucuna, Sophora tomentosa, and Vigna lutea, all belonging to the Leguminosæ; and to these we must add the seeds of Hibiscus tiliaceus and of Ipomea pes capræ, and the seedlings of Rhizophora and Avicennia. (Avicennia occurs in tropical Asia, but not in Polynesia.) The distinctive characters of the beach-drift of both coasts of America and of the west coast of Africa would be shown in the presence of seeds of Anona paludosa, the fruits of Laguncularia racemosa, Conocarpus erecta, Spondias lutea, and other plants. But the beach-drift of the American region is much more scanty. Of the shore plants generally dispersed in this region there could not be more than a couple of dozen that are indebted for their wide dispersal to the currents, and these alone figure in the effective beach drift. In the Asiatic region these plants would number at least seventy or eighty.

Summary.

(1) Effective dispersal by currents is mainly restricted to warm latitudes, as is indicated by the scanty character of the seed-drift stranded on the beaches of the south of England, Scandinavia, the Mediterranean, and Southern Chile.

(2) The present distribution in temperate latitudes of littoral plants possessing buoyant seeds or seed-vessels is to be attributed more to the influence of geographical and climatic conditions than to the agency of currents. With some of them, such as those that occur on both sides of North America, it is evident that their distribution antedates the present climatic conditions within the Arctic Circle.

(3) Time has gathered on an English beach current-dispersed plants that could tell us strange stories of many latitudes.

(4) The seed-drift that is often found in such abundance in tropical seas is partly brought down by rivers and partly swept off the coast. Very little of the seed-drift brought down by the rivers from the interior is of any service for plant-dispersal, nearly all the floating seed-drift found at sea which has any effective value being derived from the plants of the beach and of the mangrove belt.

(5) The tropical beach drift of the Old and New Worlds reflects the characters of the littoral floras of those regions, more especially with regard to the plants provided with buoyant seeds or seed-vessels. The plants represented in the beach drift common to both these regions belong mostly to the Leguminosæ. The large fruits so characteristic of Old World beach-drift are not found in the New World. The number of shore plants with buoyant seeds or seed-vessels that are widely dispersed in the American region are only one-quarter or one-third of those in the Old World region; and this difference is reflected in the scanty character of tropical American beach-drift.

CHAPTER XXX

THE VIVIPAROUS MANGROVES OF FIJI

RHIZOPHORA AND BRUGUIERA

Rhizophora.—Represented by Rhizophora mucronata, Rhizophora mangle, and the Selala, a seedless intermediate form.—Their mode of association and characters.—The relation of the Selala.—Polyembryony.—The history of the plant between the fertilisation of the ovule and the detachment of the seedling.—Absence of a rest period.—Mode of detachment of the seedling. Capacity for dispersal by the currents.—*Bruguiera.*—The mode of dispersal.—Peculiar method of fertilisation.—Length of period between fertilisation and the detachment of the seedling.—Mode of detachment of the seedling.—Summary.

BETWEEN 1897 and 1899 I made numerous observations on the Fijian species of Rhizophora and Bruguiera (mostly around the coasts of Vanua Levu and in the Rewa delta); and these were supplemented in the early part of 1904 by observations on the first-named genus in Ecuador. I did not make any collections in Fiji until Prof. Schimper asked me to obtain specimens; and a fair-sized collection containing specimens dried, and preserved in spirit, was sent to him. His illness and death shortly followed, and I lost the advantage of his great experience in these matters. In a letter written to me in 1898 he expressed the hope that I would publish my notes on the mangroves of Fiji. Years have since passed by, and as I read again his words of encouragement I take up once more the interrupted task.

RHIZOPHORA

Of the three species of this genus, two of them, Rhizophora mucronata and R. conjugata, are Asiatic and are unknown in

America ; whilst the third, R. mangle, was until recently regarded as peculiar to the American and West African regions.

When Mr. Hemsley wrote the Report on the Botany of the Challenger Expedition he remarked (iii, 149) that the American Rhizophora (R. mangle) appeared to be restricted to that region, and he questioned its existence in the Pacific Islands as indicated by Jouan for New Caledonia. The same view was taken by Prof. Schimper in his work on the Indo-Malayan strand-flora published in 1891. There was, in fact, much to support this view, since Dr. Seemann, one of the most accomplished botanists who have explored the Pacific, describes only the Asiatic Rhizophora (R. mucronata) in Fiji, and nothing is said of any other species collected by the United States Exploring Expedition under Wilkes in Fiji and Samoa.

However, in a paper on the flora of Tonga, read before the Linnean Society in 1893, Mr. Hemsley includes the American mangrove, Rhizophora mangle, amongst the collections made there by Mr. Lister ; and he refers to its occurrence also in Stewart Island (I suppose in the Solomon Group), but he suggests that it was accidentally introduced with ballast in both these localities. In 1897 I found a species of Rhizophora, to all appearances identical with the American species, in great abundance in the Rewa delta in Fiji. Subsequently the same mangrove came under my notice as the prevailing species in Vanua Levu in the same group ; and on sending photographs of a branchlet in flower and fruit and of the germinating fruit to Prof. Schimper he expressed the opinion that they belonged to the typical Rhizophora mangle.

There are four typical mangroves in Fiji, namely (1) Bruguiera rheedii, the "Dongo" proper of the natives ; (2) Rhizophora mangle, usually known as "Tiri-wai," that is to say, the Tiri of the river, or rather of the estuary ; (3) Rhizophora mucronata, the "Tiri-tambua" of the Fijian, signifying the Whale's Tooth Tiri in allusion to the form of its fruit ; and (4) a seedless form intermediate between the two species of Rhizophora, which the Fijians designate "Selala," a name signifying "the tree with empty flowers."

Bruguiera rheedii and Rhizophora mucronata were alone recorded by Dr. Seemann and his predecessors ; but he significantly refers to the natives speaking of four mangroves. Mr. Horne, who spent twelve months in the group some years later, also overlooked the American Rhizophora ; but it is apparent that both these botanists were naturally more interested in the vegetation of the

inland regions than of the coast swamps, and we have before observed that they failed to record Scirpodendron costatum, a giant-sedge very common and conspicuous in the swamps. It is not easy to understand Dr. Seemann's remark that "mangroves are restricted to but few parts of the larger islands." Horne, who was in the islands eighteen years afterwards, makes frequent allusion to them. The natives whom I questioned closely on this subject scouted the idea that any of the four mangroves above named were recent arrivals. The coasts, as they said, had always been extensively fringed by mangroves; and the reader has only to refer to my remarks in the second chapter of my volume on the geology of Vanua Levu to convince himself that mangrove swamps of considerable extent existed in the time of Commodore Wilkes (1840).

The Relative Abundance and Mode of Association of the three Fijian forms of Rhizophora.

Stated in their order of frequency, we have first Rhizophora mangle, the American species, then Rhizophora mucronata, the Asiatic species, and lastly the Selala. The first is equally at home at the sea-border and on the banks of brackish estuaries. The second is, as a rule, more exclusively at home on the sea-coasts; and the same may be said for the Selala. Usually all three kinds occur in the lower part of an estuary; but as we ascend the river and the water freshens, the Asiatic Rhizophora and the Selala disappear, and the American plant is alone found in the higher reaches, where the density of the water ranges according to the state of the tide between 1·000 and 1·010. I examined the distribution of these three forms of Rhizophora in numerous estuaries of Vanua Levu, as well as in the Rewa estuary in Viti Levu; and it was ascertained that in all cases they followed the rule above indicated. When the estuary receives but few streams and the water is mostly salt, the three Rhizophoras may extend miles inland; but when it contains a large body of fresh-water, Rhizophora mangle may be the only form observed from the mouth of the river to the head of the estuary, and it may monopolise the adjacent coasts. On the other hand, Rhizophora mucronata may occupy almost exclusively a long extent of coast; or the Selala may prevail in certain localities, as on parts of the Mathuata coast of Vanua Levu.

The manner of association of these three Rhizophoras is of

interest in connection with the origin of the seedless Selala. They very rarely occur mingled together, but grow gregariously in contiguous colonies ; and not uncommonly all three may occur on the same line of coast within a distance of a few hundred yards. The colonies pass into each other without a break, and there is no fixed rule of association. Whilst on the south side of Vanua Levu the Selala is generally associated with the American Rhizophora, on the north side it is usually in touch with the Asiatic species. In other localities all three occur in contiguous colonies. The Selala colony may be exposed on the line of a river-bank or along the sea-coast, or it may lie in the heart of an extensive mangrove tract. The most extensive mangrove region in Fiji, that of the Rewa delta, is in great part occupied by Rhizophora mangle ; but all three forms grow together in the eastern part of the delta ; and here, strangely enough, as at Daku, the Selala may grow sporadically, and all three may grow mixed together with their branches intercrossing.

The Characters of the Selala or Seedless Rhizophora compared with those of the American Mangrove (R. mangle) and the Asiatic Mangrove (R. mucronata).

The three kinds of Rhizophora, when seen at the same time along a tract of coast, may be readily distinguished by the different shades of green of their foliage, that of Selala being dark green, that of Rhizophora mucronata light green, and that of Rhizophora mangle intermediate in shade. The Selala is usually the tallest of the three, and attains a height of from 20 to 30 feet or even 40 feet and over, the aërial roots dropped from the higher branches giving it a characteristic aspect. Rhizophora mangle is generally the shortest, and at the coast is from 10 to 12 feet high ; but where the mangrove vegetation is most luxuriant, as in the great swamps in the interior of the Rewa delta, it forms tall trees as much as 40 feet in height, displaying the aërial roots hanging from the higher branches. Rhizophora mucronata is, as a rule, intermediate in height, and is distinguished by its stout, reddish trunk and reddish aërial roots.

The trunks of Selala are often in an inclined position and supported entirely by the trestle-like aërial roots, the lower end raised some 5 or 6 feet above the ground with the rest of the trunk inclined upwards. They then look like gigantic walking-stick insects. The same habit may be sometimes observed with the larger trees of Rhizophora mucronata, and in fact all three may

present at times the same habit of growth. The taller trees of Rhizophora mangle may resemble the Selala in habit, and the smaller trees of the Selala may approach the habit of Rhizophora mangle.

The distinctive characters of the Selala are given in the table opposite. It will be there seen that this form is intermediate between the other two species as regards the form and size of the petioles and peduncles; the size of the bracts and bracteoles; the colour, form, and size of the flowers; and in the length of the style. Its leaves are smaller than in the case of the other two species, but pointed and semi-aristate like those of Rhizophora mucronata. There are, however, two varieties of the Selala, both with larger foliage than that belonging to the prevailing type of the tree, and from 10 to 15 feet in height. In one the flowers are more numerous, each flowering stem branching four or five times and bearing at least twenty-four flowers, the first branch being trichotomous and the rest dichotomous. In the other, which is the prevailing form on the Mathuata coast, there is a nearer approach to Rhizophora mucronata in the rounding of the peduncles and in the length of the style. Then, again, there are divergent varieties of Rhizophora mangle which in the larger bracts and bracteoles and in the greater size, form, and paler hue of the flowers come nearer to the Selala. Taking all the characters together, the Selala, though intermediate between the Asiatic and the American species, comes in the most critical diagnostic points, as in the inflorescence, in the individual flowers, and in the form of the apex of the leaf, nearest to Rhizophora mucronata, the Asiatic species.

The seedless character of the Selala is well known to most Fijians of the coast districts, the native name signifying empty (lala) flowers (se). Now and then they aver that it produces fruit, but the numerous offers of rewards in money never resulted in their bringing me the fruits. During my residence of two years in the group I examined the Selala trees in a great number of localities and never succeeded in finding them in fruit.

With all three kinds the anthers burst in the bud before it begins to open, and we may ask why the process of self-fertilisation, which is effectual with the other two kinds, produces no result with the Selala. In all three cases the flower-buds and expanded flowers hang downwards, and the expanded flowers retain their parts for the first twenty-four hours, the pollen being caught in quantity on the hairy edges of the petals. During the next day the withering stamens fall out, and on the following day the petals fall too. With the Selala, the style soon begins to blacken and

Characters.	Fiji.			Ecuador.	
	Rhizophora mucronata.	Selala (a seedless form).	Rhizophora mangle.	Rhizophora mangle (Mangle chico).	Rhizophora mangle (Mangle grande).
Height of tree in feet ...	12—20.	20—40.	9—12.	10—15.	50—80 and more.
Colour of foliage	Pale green.	Dark green.	Intermediate shade.	Pale green.	Dark green.
Base of leaf...	Tapering.	Sub-rounded.	Tapering.	Tapering or sub-rounded.	Tapering.
Apex of leaf	Acute, and terminating in a twisted point a line (2·5 mm.) long.	Acute, and terminating in a twisted point less than a line (2·5 mm.) long.	Very obtuse, with no twisted point.	Very obtuse, with no twisted point.	Very obtuse, with no twisted point.
Leaf-stalk (petiole)	Rounded, 1–1$\frac{2}{10}$ inch, (25–30 mm.) long, about as long as the peduncle.	Rather flattened horizontally, 5–8/10th inch (12—20 mm.) long, shorter than the peduncle.	Length as in Selala, but flattening very marked.	Flattened above and below, with no median groove, ½ inch (12 mm.) long; not half as long as the peduncle.	Flat above with a median groove, 1 inch (25 mm.) long, two-thirds the length of the peduncle.
Inflorescence	Branching (dichotomous) two or three times with four to eight flowers.	Branching usually twice, but sometimes three times; first branching trichotomous, rest dichotomous; six to twelve flowers; in one variety, flowers as many as twenty-four.	Usually branching only once (trichotomous) and bearing only three flowers; but sometimes branching again (dichotomous) and bearing then six flowers.	As described under R. mangle of Fiji.	Branching at least three times, sometimes four or five times, trichotomous or dichotomous, twelve to forty-eight flowers.
Peduncle (lowest flower-stalk)	Rounded.	Flattened above.	Flattening more marked than with Selala.	Sub-angular.	Rounded.
Pedicels	As stout as the peduncle, and rounded.	More slender than the peduncle, and angular.	As in Selala.	More slender than the peduncle, and rounded.	More slender than the peduncle, and angular.
Bracts and bracteoles ...	Large, 1½ line (4 mm.).	Small, ⅔ line (2 mm.).	Very small or absent.	Scarcely developed, ½ line (1 mm.).	Well developed, 1 line (2·5 mm.).
Calyx	Very pale yellow, or dirty white, rounded at base in the bud, lobes 4½–5 lines (11–12 mm.).	As in R. mucronata.	Pale or bright green, angular at base in the bud, lobes 3½ lines (8 mm.).	As with R. mangle of Fiji.	As with R. mucronata and Selala of Fiji, but lobes 4 lines (10 mm.).
Length of style	1½ lines (4 mm.).	1 line (2·5 mm.).	½ line (1·5 mm.).	Less than a line (2·5 mm.).	1½ lines (4 mm.).
Fruit	Ovoid and usually symmetrical, with large persistent bracteoles at base. (Hypocotyl 16 inches.)	No fruits produced.	Conical, somewhat curved, and thus not symmetrical; bracteoles at base very small or absent. (Hypocotyl 9 or 10 inches.)	As in R. mangle of Fiji. (Hypocotyl 9 or 10 inches.)	Conical, not symmetrical, and somewhat curved; large persistent bracteoles at base as in R. mucronata. (Hypocotyl 12 to 15 inches.)
Colour of trunk, rootstock and roots	Reddish.	—	—	—	—

wither, and in a few days the flower becomes detached and drops off. With Rhizophora mucronata and Rhizophora mangle, the style preserves its healthy condition, and shortly evidences of fertilisation appear in the altered shape of the ovary. It is apparent, therefore, that in the case of the Selala fertilisation has not occurred, although the mechanical processes connected with it have been carried out. The cause of this is not far to seek.

Although the ovaries of the Selala contain four ovules, which in size and appearance do not differ from those of Rhizophora mangle and R. mucronata, its pollen when compared with that of the other two forms presents a remarkable difference. The pollen of these three mangroves was examined in five localities far apart from each other, and in all the same results were obtained. The pollen-grains of the Selala are much smaller than those of the other two, and differ much from them in form. They are irregularly oval in outline, and have a shrunken look beside the spherical symmetrical grains of the two species with which they are compared. They are from one-fourth to one-third the size of those of Rhizophora mucronata, and from one-third to one-half the size of those of Rhizophora mangle.

There is much to support the view that the Selala is a cross between the other two species, its intermediate characters and its seedless condition being especially indicative of such a derivation; but there are several difficulties in accepting this explanation.

(1) The circumstance of the anthers bursting in the flower-bud would considerably lessen the chances of cross-fertilisation; but this objection is not insurmountable, since numerous insects, such as flies, ants, and small coleoptera, visit the newly opened flowers, and they might sometimes produce a result. When I made this suggestion to Prof. Schimper he replied that insect-pollination was quite possible after the expansion of the flowers.

(2) If, as seems highly probable, the pollen of Selala is impotent and the ovules fertilisable, then its seedless condition implies not only an incapacity for self-fertilisation, but also for cross-fertilisation; and if Selala with its impotent pollen does not admit of cross-fertilisation, this would still less be expected of Rhizophora mucronata and R. mangle where the pollen is potent and where fertilisation takes place in the bud. I endeavoured to fertilise the Selala flowers with the pollen of the two other species; but there were no results, the flowers falling off in a few days. It may here be remarked that on one Selala tree I found a solitary flower with an enlarged ovary, as if through fertilisation.

(3) It is not easy to explain the gregarious growth of the Selala if it is a seedless hybrid. The colonies could not be renovated by mere intercrossing, especially in places where, as on the north coast of Vanua Levu, the dense belt of mangrove is for many miles composed in mass of Selala trees, with a few trees of the Asiatic and American Rhizophoras growing on the outskirts.

It is obvious that in order to clear the way for considering this problem the means of renovating the Selala colonies should be inquired into. In the first place, whilst seedlings occur in numbers under the trees of the other two Rhizophoras they are never to be found under the Selala trees. The mode of reproduction of the Selala is evidently vegetative, and the question arises as to what mode of vegetative reproduction occurs. The Selala trunks, as already observed, are often inclined, the trunks being supported on trestle-like aërial roots. These trunks send out branches which in their turn drop aërial roots ; and when the decay of the parent trunk takes place, the branches are able to live independently. The primary branches in due time send out secondary branches which also let fall aërial roots ; and thus the process is repeated indefinitely, the result being a maze of semi-prone trunks, branches, and aërial roots. The first stage of the process ends with the death of the parent trunk, and the primary branch, supported by its own aërial roots, is often all that the observer can distinguish in the centre of a colony. This is evidently the mode by which the Selala colonies are renovated in their interior. One sometimes observes in the midst of one of these colonies extensive bare mud-flats 100 to 500 yards across from which apparently the trees have died off *en masse*. The natives assert that when part of a Selala tract is cleared the trees never grow again.

But *pari passu* with this process of vegetative reproduction of the Selala, by which the mass of the colony is preserved and renovated, there is evidently some other process of reproduction in operation amongst the trees of Rhizophora mangle and R. mucronata at the edge of the colony, as a result of which Selala seedlings are produced. Whilst no seedlings are to be observed striking into the mud under the Selala trees, numbers occur, as before observed, under the trees of the other two species. Those under the trees of R. mangle possess in nearly all the cases the distinctive leaf-characters of that mangrove, and would be recognised at once as belonging to that species. On the other hand, those beneath the trees of R. mucronata are of two kinds, some of them being readily recognised by their foliage as of the Selala type

others, again, being typical seedlings of R. mucronata. Only those seedlings, or "keimlings" as we might term them, were noted that had dropped plumb from the branches above.

Such were the results of my investigations on Vanua Levu. My field of inquiry was then shifted to the Rewa delta, where, with the assistance of the Daku natives, who, like most Fijians, display a keen interest in matters relating to their plants, I spent a few days in investigating the origin of the Selala trees that grow sporadically in that locality. On pulling up some of the young trees we found that the original radicular or hypocotyledonary portion of the keimling could be still distinguished. My zealous native friends also pointed out to me that though the leaves in form and colour were those of the Selala, the rootstock was reddish like that of R. mucronata, and not white as with R. mangle. The natives averred that the Selala trees are produced in the first place from fruits of R. mucronata. When young, they said, they are Tiri-tambuas (R. mucronata), but when old, Selalas. Yet although R. mucronata may be now regarded as the source of the Selala trees, and my Vanua Levu observations pointed unmistakably in this direction, it could not be definitely settled whether this was the result of a cross with the male element of R. mangle or whether the Tiri-tambua (R. mucronata), in producing two types of seedlings, one fertile with the parent characters and the other seedless of the Selala type, brought about the same end. On the whole I am inclined to the view that the Asiatic Rhizophora presents us in the dimorphism of its seedlings the true explanation.

This inference is supported by the behaviour of Rhizophora mangle on the coast of Ecuador, a subject which is discussed in Chapter XXXII, and I have given the results of my observations on the Ecuadorian Rhizophoras side by side with those on the Fijian trees in the table before given. There are two very distinct forms of the American Rhizophora (R. mangle) in the swamps of Ecuador. There is the low coast tree, the "Mangle chico" of the Ecuadorians, ten to fifteen feet in average height, which grows on the sea-front of the swamps and has all the general appearance and the more conspicuous characters of the American Rhizophora in Fiji. There is also a tall tree, 60, 80, or even 100 feet high, that forms the great mass of the mangrove swamps. In its inflorescence, in the dark green colour of its foliage, and in other characters, it comes near the Fijian Selala; but it differs in fruiting abundantly. This is locally termed the "Mangle grande," and its true relation to the Fijian Selala appears to be as follows. Whilst

both as regards the flowers approach the Asiatic Rhizophora (R. mucronata), the Fijian Selala resembles the Asiatic tree also in its foliage, whilst the "Mangle grande" or the Ecuadorian Selala more resembles the typical American tree (R. mangle) in its leaves and also in its seedlings. Here in the Ecuadorian swamps there can be no question of crossing, since both, according to Baron von Eggers, belong to one species. Therefore I am inclined to the opinion that whilst the Asiatic Rhizophora displays dimorphism in Fiji, the American Rhizophora displays dimorphism in Ecuador. The reversion on the part of the "Mangle grande" of Ecuador to some of the characters of the Asiatic plant is remarkable, and points to the greater antiquity of the Asiatic R. mucronata as compared with the American R. mangle.

This accords with the opinion expressed by Schimper in his work on the Indo-Malayan strand flora that the American Rhizophora is either a degenerated descendant of the Asiatic R. mucronata or a sister form derived from a common ancestor. America, as we have seen, possesses only one of the three species of Rhizophora, and this is the only representative that it owns of the four Asiatic genera (Rhizophora, Kandelia, Ceriops, Bruguiera) that constitute the tribe Rhizophoreæ. The rule prevailing with current-dispersed plants that America is a distributor and not a recipient evidently does not apply to the Rhizophoreæ; and to explain their distribution we must go back to some epoch very remote from the present. That Fiji derived its representatives of Rhizophora mangle from America by the agency of the currents I do not for a moment admit. The restriction of the species and indeed also of the genus to the Western Pacific is very significant. It is far more likely that, as I have pointed out in the case of Lindenia (see page 396), the American Rhizophora was once widely distributed over the tropics of the Old and New Worlds, and that it is now on the "down grade" towards extinction. Its survival in the Western Pacific could thus be explained without our being obliged to suppose that the seedlings or keimlings have been carried uninjured across the Pacific Ocean, an ocean voyage for which, as shown in a later page, they are not well fitted.

The Occasional Occurrence of more than one Seed in the Fruits of Rhizophora mucronata and Rhizophora mangle (Polyembryony).

The bilocular ovary contains four ovules, one of which only as a rule becomes a seed. But it is incorrect to say that the fruits are

always one-seeded, since two or even three seeds are occasionally produced, and they may all germinate. In November, 1897, I noted eight hundred fruits of Rhizophora mangle germinating on the trees in one of the creeks of the Rewa delta. Out of this number eight fruits had two germinating seeds and one had three, the protruding radicles being in all stages of growth. Just two years afterwards I counted eight hundred more fruits in the same locality, and then observed seven with two germinating seeds and none with three, the radicles protruding in all cases. On another occasion at Wailevu in Savu-Savu Bay I counted four hundred, and none had more than a single radicle protruding. The results appear to vary with the locality, but in the Rewa creek the proportion of fruits in which more than one seed germinated was fairly constant at dates two years apart, namely, about one per cent. Occasionally, however, in particular localities a greater proportion may be noticed. Thus near Daku in the Rewa delta I found that the proportion was between two and three per cent. for the same species (R. mangle), those with three germinating seeds being about half per cent.

The case of more than one seed germinating in the fruits of Rhizophora mucronata never came under my observation ; but in one locality, where I examined a considerable number of fruits near the stage of germination, between ten and fifteen per cent. showed two seeds approaching maturity.

Warming thoroughly investigated the polyembryony of Rhizophora more than twenty years ago, seemingly from materials brought to him from the West Indies (Engler's *Botanische Jahrbücher*, band iv., 1883). With the usual German thoroughness he deals with the work of earlier observers, and goes back to Piso in the middle of the 17th century. Of the four ovules, he remarks, three usually abort, and only in rare cases are two seeds developed. He quotes Baron von Eggers to the effect that only in three per thousand cases was more than one seedling observed protruding from a germinating fruit. These remarks evidently all apply to the American species. I do not find any reference in my notes to polyembryony in Ecuador, and evidently its occurrence is not so frequent there as in Fiji.

It is frequently apparent in the cases where more than one seed germinates in a fruit that on account of the difference in the length of the protruding seedlings germination does not always begin at the same time. Thus in Fiji the difference in the length varied between one and three inches, an amount representing at least from ten to twenty days' growth, as will be subsequently pointed out.

Warming in one of his figures gives a fruit where an interval of some months seems to be indicated, since one of the seedlings has fallen out and the other is protruding less than an inch. By cutting across a fruit containing two seeds one may sometimes observe one seed quiescent and the other beginning to germinate. The significance of this occasional interval between the germination of seeds in the same fruit will be referred to in a later page.

The Seasons of Flowering and Fruiting of the Species of Rhizophora in Fiji.

The Selala flowers all the year. With the two American and Asiatic species there are considerable variations between different localities. Generally speaking, they flower and fruit all the year through; but the flowers are usually less abundant in the warm season from December to February, and the germinating fruits which are to be observed on the trees every month of the year are more numerous in that season.

The History of the Reproductive Process in Rhizophora from the Fertilisation of the Ovule to the Falling of the Plantlet or Seedling from the Tree.

I devoted great attention to this subject in the instance of Rhizophora mangle, being desirous of determining two points, in the first place as to whether there was any period of rest between the maturation and germination of the seed, and in the second place as to the period that elapsed between the commencement of germination and the fall of the seedling.

The principal change in the ovary for the first three or four weeks after fertilisation is shown in its increased breadth. The increase in height is but slight during this period; and in fact after thirty days the ovary only added 2 millimetres to its original height of 3 millimetres. After this the growth of the fruit proceeds until the tip of the radicle pierces its summit, the fruit being then about eleven lines (2·8 cm.) long. *From the date of fertilisation to the time the radicle pierces the top of the fruit a period of about fifteen weeks elapses.* (The fruit, it should be here remarked, continues to grow in length and breadth after the radicle has protruded, attaining a length of thirteen or fourteen lines [3·5 cm.] when the seedling or "keimling" is ready to fall.)

By referring to the table below it will be observed that there is no period of rest in the growth of the fruit up to the date of the protrusion of the radicle. It will now be shown that there is normally no pause between the epoch of the maturation of the seed and the beginning of germination, or, in other words, that from the time of the fertilisation of the ovule to the onset of germination there is no cessation in the process of growth of the embryo. That period of dormant vitality which almost all seeds pass through forms no normal feature in the life-history of this species of Rhizophora.

Rhizophora mangle and R. mucronata.

Rhizophora mangle.	
Growth of fruit in height.	
Lines or tenths of an inch (millimetres in brackets).	Number of days since fertilisation.
2 (5)	30
3 (7·5)	42
4 (10)	50
5 (12·5)	61
6 (15)	67
7 (17·5)	74
8 (20)	83
9 (22·5)	92
10 (25)	100
11 (28)	105
	107 { Protrusion of the hypocotyl
Growth of the protruding hypocotyl.	
10 (25)	127
20 (50·5)	141
30 (76)	151
40 (101·5)	160
50 (127)	167
60 (152)	175
70 (177·5)	185
80 (203)	202
90 (228)	222
	229 { Fall of the seedling

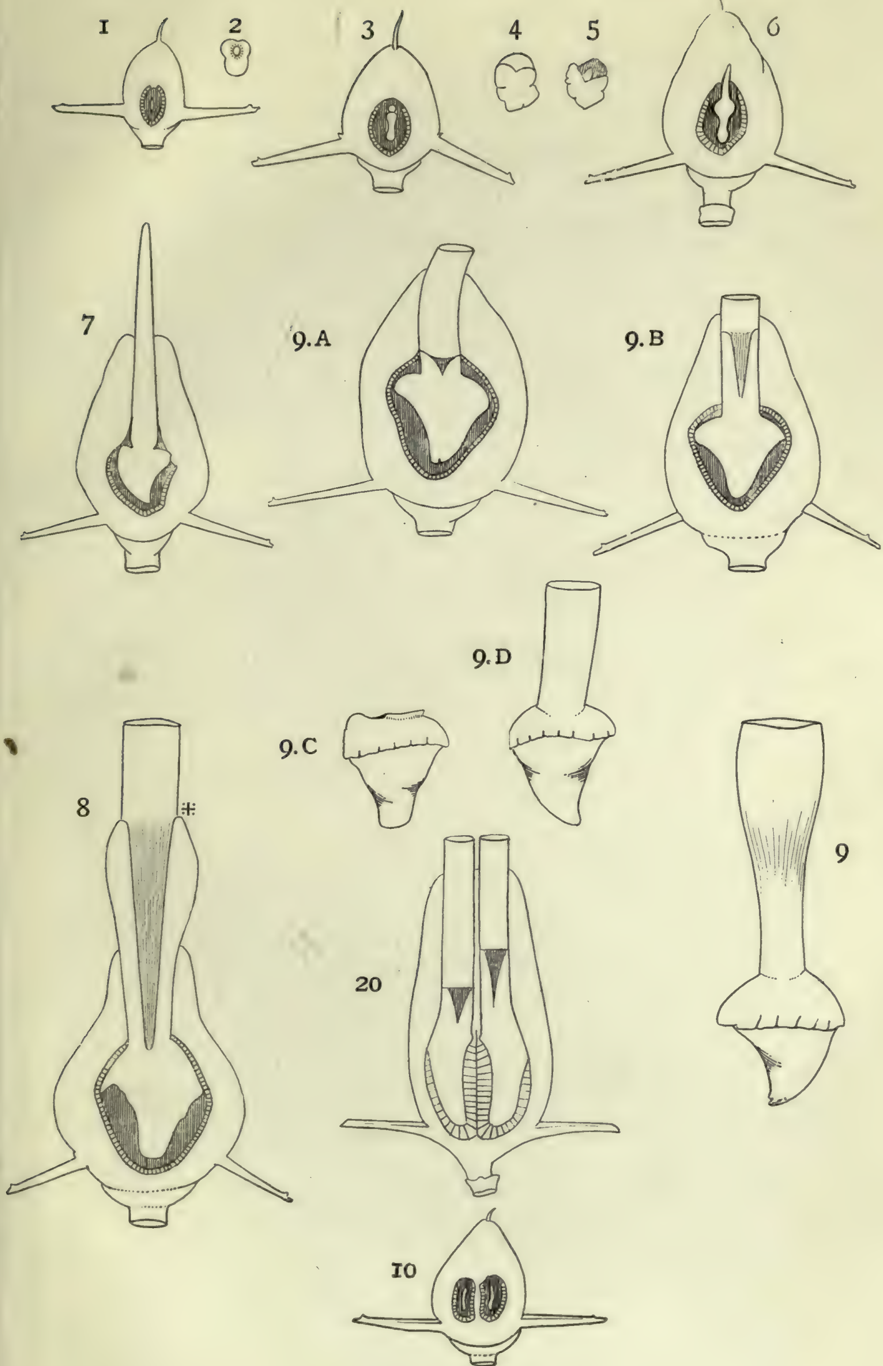
Explanation of the Table.

We have here shown the period between fertilisation and the fall of the seedling from the tree.

This period divides itself into two parts, the first being concerned with the continuous growth of the fruit and of the inclosed embryo until the tip of the hypocotyl appears through the apex of the fruit, the second being indicated by the growth of the protruding hypocotyl until the fall of the seedling.

The height of the fruit is measured from the base of the calyx-lobes, and the length of the hypocotyl at first from the apex of the fruit and afterwards from the edge of the protruding neck of the cotyledonary body. The height of the ovary at the time of fertilisation is about 3 millimetres; and from that time onward it is to be regarded as a fruit.

[*To face page* 452.



FIGURES ILLUSTRATING THE DEVELOPMENT OF THE SEED AND THE GERMINATING PROCESS OF RHIZOPHORA AND BRUGUIERA

(Natural size. Drawn for convenience of description in the erect position.)

1.	Rhizophora mucronata .	Fruit $3\frac{1}{3}$ lines (8–9 mm.) high, six to seven weeks after fertilisation. The micropyle is but slightly dilated, and is occupied by a small plug of endosperm.
2.	,, ,,	Seed of fruit represented in Fig. 1.
3.	,, ,,	Fruit 5 lines (12 mm.) high, eight to nine weeks after fertilisation. Germination is about to begin. A large plug of endosperm now protrudes through the dilated micropyle, but still covers the lengthening hypocotyl.
4., 5.	,, ,,	Seed of fruit represented in Fig. 3. In Fig. 4 the plug of endosperm is shown on the upper end of the seed ; whilst in Fig. 5 it has been removed, exposing the tip of the hypocotyl.
6.	,, ,,	Fruit $7\frac{1}{2}$ lines (18 mm.) high, eleven to twelve weeks after fertilisation.
7.	,, ,,	Fruit, seventeen or eighteen weeks after fertilisation.
8.	,, ,,	Full-grown fruit with upper portion of seedling just before detachment from the tree. The long tapering plumule is here inclosed in the cotyledonary body. The ∗ indicates the point of detachment of the seedling.
9.	,, ,,	The cotyledonary body of Fig. 8.
9A., 9B., 9C., 9D.	,, ,,	Illustrating different stages in the development of the plumule and of the neck of the cotyledonary body resulting finally in the expulsion of the plumular end of the seedling from the fruit cavity as in Fig. 8. (See page 458.)
10	,, ,,	Fruit with two seeds.

FIGURES ILLUSTRATING THE DEVELOPMENT OF THE SEED AND THE GERMINATING PROCESS OF RHIZOPHORA AND BRUGUIERA—(*continued*)

(Natural size. Drawn for convenience of description in the erect position.)

11.	Rhizophora mangle . .	Fruit, six weeks after fertilisation.
12.	,, ,,	Seed with plug of endosperm, as shown in Fig. 11.
13.	,, ,,	Fruit, eight weeks after fertilisation. The tip of the hypocotyl is now piercing the plug.
14.	,, ,,	Embryo (enlarged) shown in Fig. 13.
15.	,, ,,	Fruit, ten weeks after fertilisation. The growing hypocotyl has now pierced the plug.
16.	,, ,,	Embryo shown in Fig. 15.
17.	,, ,,	Fruit, nearly sixteen weeks after fertilisation.
18.	,, ,,	Full-grown fruit, just before the detachment of the seedling from the tree. The long tapering plumule is inclosed in the tube of the cotyledonary body. The point of detachment of the seedling is indicated by ∗.
19.	,, ,,	The cotyledonary body of Fig. 18.
20.	,, ,,	Fruit with two seedlings in different stages of growth (given in the first plate).
21.	Bruguiera Rheedii . . .	Fruit, about four weeks after fertilisation. (The shaded portion is the calyx-tube or cup, in the midst of which rises the style.)
22.	,, ,,	Germinating seed.
23.	,, ,,	Germinating fruit, about eight weeks after fertilisation.
24.	,, ,,	Germinating fruit, about ten weeks after fertilisation. Here the growing hypocotyl, carrying the style with it, has pushed upwards the lining membrane of the floor of the calyx-tube, which has ruptured and forms a cap on its extremity.
25.	,, ,,	Germinating fruit, thirteen or fourteen weeks after fertilisation.
26.	,, ,,	Fruit with full-grown seedling just before its detachment from the tree.

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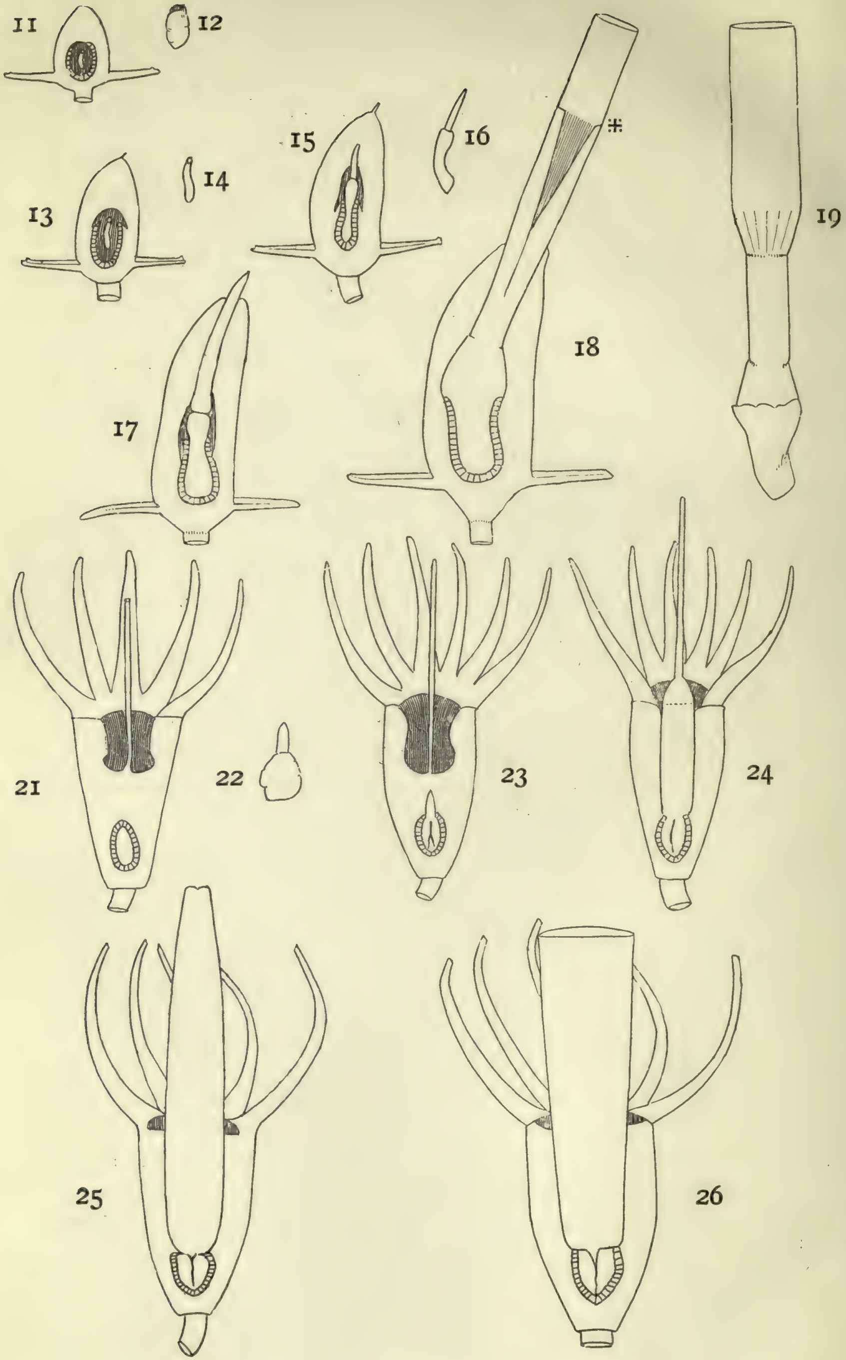

RHIZOPHORA MUCRONATA.

Growth of the first seven inches of the hypocotyl after it protrudes from the fruit.

10 lines	(25 mm.)	after	26	days
20 „	(50·5 mm.)	„	41	„
30 „	(76 mm.)	„	51	„
40 „	(101·5 mm.)	„	61	„
50 „	(127 mm.)	„	70	„
60 „	(152 mm.)	„	78	„
70 „	(177·5 mm.)	„	86	„

In my description of the germinating process of Rhizophora mangle from this particular standpoint I adopt the general views of Prof. Schimper, the observations being my own, the phraseology employed being his. It would be out of place here to deal with the biological significance of a process to which observers like Warming, Goebel, Karsten, Schimper and Haberlandt have applied their greater talents as well as their greater experience. I investigated the subject carefully from my own standpoint of inquiry, and whilst the reader will find in my rough sketches of the various stages of the process a little aid in following the argument, he is referred for detailed treatment of the subject to the memoirs of the above-named botanists as well as to those of yet more recent investigators.

After fertilisation, according to Prof. Schimper (*Ind. Mal. Strand-flora*), the embryo-sac is filled with endosperm, which subsequently protrudes and forms a plug completely closing the micropyle (see my figures). As my observations showed, the seed during the first eight weeks after fertilisation increases continuously in size, and the plug of endosperm, at first inconspicuous, becomes of considerable size, the seed attaining a length of seven millimetres. The embryo meanwhile grows rapidly, and at the end of this period of eight weeks the radicular tip or the point of the hypocotyl begins to protrude from the micopyle, still covered by the plug of endosperm, the fruit being between four and five lines (10-12 mm.) in length (figures 11-14). In another week, when the fruit has grown another line in length, the tip of the radicle is on the eve of piercing the plug, and this may be rmed *the commencement of germination, nine weeks after the act of rtilisation.* The next stage, after an interval of one and a half weeks, is illustrated in figure 15; and *after a period of about fifteen weeks from the date of fertilisation the tip of the radicle pierces the*

top of the fruit. As shown in the figures, the fruit grows in length throughout the process.

The question as to whether the matured seed passes through a stage of quiescence before it germinates finds its answer in the statement that only nine weeks elapse between fertilisation and germination. It may, however, be urged that the maturation of the seed could be accomplished in a few weeks, and that after this a period of dormant vitality might follow. This objection can be at once disposed of and the whole matter placed beyond reasonable doubt by making, as I did, a large number of vertical sections of the fruit in all its stages. It will then be perceived that there is a fairly constant relation in all stages of growth between the seed and the fruit, whether maturating or germinating. Since the growth of the fruit is continuous (see Table) up to the time of the protrusion of the tip of the hypocotyl through its coats, it follows that there can be no appreciable pause between the completion of maturation and the commencement of germination of the seed. In other words, both fruit and seed preserve the same relation during the process, and the absence of any period of rest is to be inferred from the uninterrupted growth of the fruit.

We will take, to illustrate this point, a fruit between four and five lines long in the stage that immediately precedes germination (see figure 11), The fruit proceeds with its growth, and the seed, we will suppose, remains quiescent for a month. At the end of that time (see Table) the fruit would be eight lines long, and the seed, of course, would be unchanged. This condition of things never presented itself to me. Fruits eight lines long were always far advanced in germination (see figure 15). If the seed passes through an interval of rest before germination, it must be of a very short duration and practically *nil.*

This absence of any period of rest between the final maturation of the seed and its fertilisation had already been assumed by Prof. Schimper. Writing to me on July 14, 1898, when my observations were in progress, he says :—" I am ready to assume, according to my own experience, that there is continuous development until the falling off of the embryo. More accurate observations on the subject would be interesting, and would not present any great difficulties." At the end of the same month he wrote the preface to his great work on Plant-Geography ; and he expresses himself decidedly on this point. Speaking of Rhizophora mucronata (English edition, p. 396), he says that " the fruit. . . . soon after the completion of its growth is pierced at its summit by the green hypocotyl, as the

embryo does not undergo any period of rest, but continues to develop without interruption."

Though the rest-period is normally non-existent with the seeds of Rhizophora, it has already been observed that it is indicated in rare cases and under exceptional conditions. Thus I have already remarked that in Fiji about one per cent. of the germinating fruits of the American species exhibit more than one seed. These seeds usually begin to germinate about the same time, but in a few cases, say, one in ten, a marked difference in the length of the protruding hypocotyls points to the fact that one of the seeds began to germinate some weeks after the other. We at times also meet with fruits which when cut across display two seeds, of which only one is beginning to germinate. Such cases indicative of a pause between the maturation of the seed and the beginning of germination would be very rare. With Rhizophora mangle, probably one in a thousand fruits would be a generous estimate.

In passing it may be remarked that the same stages occur with Rhizophora mucronata in the development of the seed and in the subsequent germinating process. When the fruit is three lines long the micropyle is but slightly dilated (see figures 1 and 2). When it is four lines long the endosperm begins to escape from the gaping micropyle and forms a projecting plug. The growth of the embryo now becomes rapid, the endosperm escapes in greater quantity, and by the time the fruit is five lines long the tip of the radicle is on a level with the micropyle, although still covered by the plug (see figures 4, 5, 6). After this, germination begins; and when the fruit is six lines in length the radicle is in the act of penetrating the plug. Ultimately the tip of the radicle pierces the top of the fruit when this last is nine or ten lines long. As shown in the figures there is continuous growth of the fruit during the maturation and germination of the seed, until, in fact, the plantlet drops into the water. With reference to the stage when germination begins, it should be remarked that the formation of the large plug of endosperm outside the micropyle does not necessarily indicate the beginning of germination. Germination is in progress only when the hypocotyl or radicle begins to lengthen and is on the point of piercing the plug of endosperm that fills up the gaping micropyle. This is well shown in this species in the case of fruits with two seeds. Both seeds may have large plugs of endosperm, and yet only one may show indications of germination in the lengthening hypocotyl.

We must now return to the subject of the growth of the hanging

seedling of Rhizophora mangle. We have already remarked that, as shown in the Table, about fifteen weeks (107 days) is the average time elapsing between the fertilisation of the ovule and the protrusion of the tip of the radicle through the top of the fruit. A further period of seventeen and a half weeks (122 days) is occupied by the growth of the seedling on the tree, at the end of which period it drops into the water or mud according to the state of the tide. This gives a total period of nearly thirty-three weeks (229 days) as the duration of the time between fertilisation and the fall of the seedling. This may be divided, as has been already implied, in the following manner :—

(1) Period between fertilisation and germination.	9 weeks.
(2) Period between the commencement of germination and the protrusion of the tip of the radicle through the top of the fruit.	6½ weeks.
(3) Period occupied by the growth of the hypocotyl outside the fruit, and terminating in the fall of the seedling from the tree.	17½ weeks.
Total . . .	33 weeks.

This represents the average of numerous observations, the deviations being from two to three weeks on either side. In the latter part of its growth, the lower end of the hypocotyl becomes thickened or club-like, and during the last week or ten days the increase in length is arrested altogether.

My observations on the growth of the seedling on the tree of Rhizophora mucronata were comparatively few; but, as shown in the Table on page 453 they give nearly the same rate of growth. Taking the average length attained by the hypocotyl on the tree at sixteen inches, and employing as well the data supplied by Rhizophora mangle, a period of 26½ weeks would elapse from the time the hypocotyl pierces the top of the fruit until the plantlet falls from the tree. If we then add, as in the case of the other species, 15½ weeks for the preceding period between fertilisation and the protrusion of the hypocotyl, we get a total of 42 weeks for the whole period from fertilisation to the fall of the seedling. In the extreme cases where a length of almost two feet is attained on the tree, the period would somewhat exceed twelve months; and in those rare instances in other regions, when, according to Schimper, the seedling is a metre in length, probably eighteen months would be required. The period for Rhizophora mucronata is thus con-

siderably longer than for R. mangle, which is sufficiently indicated by the difference in the average length of their hypocotyls on the tree in Fiji, that for R. mucronata being sixteen inches, and that for R. mangle nine or ten inches.

The only other observations that have come under my notice relating to this subject are those made by Jacquin on Rhizophora mangle in the West Indies in the middle of the eighteenth century. The results are literally quoted by Warming ; but I have referred to the original account in the work of Jacquin, entitled *Selectarum Stirpium Americanarum Historia*, Vindobonæ, 1763. According to this observer the seedling falls from the tree in the twelfth month from the fecundation of the flower. This happened in my observations on the same species in Fiji in the eighth or ninth month. Jacquin states that the tip of the radicle protrudes from the fruit in the third month, whilst my results give it as taking place in the fourth month. The difference in the length of the total period, it may be remarked, would be to a great extent determined by the varying length acquired by the seedling before it drops from the tree. In ordinary conditions it averages about ten or eleven inches, and the hypocotyl itself attains a length of nine or ten inches on the tree, both in Fiji and Ecuador ; but in sheltered localities it may attain a length half as long again. I have already pointed out in the case of the fruits of Rhizophora mucronata that a year and more would be sometimes required, and the same remark would apply to unusually long fruits of R. mangle. Local conditions would often produce varying results, both in the rate of growth of the hanging seedling and in the duration of the period of its attachment to the tree ; but it is probable that nine or ten months would represent for the genus the average length of the period between fertilisation of the ovule and the detachment of the seedling from the parent tree.

The mode of separation of the seedlings of Rhizophora mangle and Rhizophora mucronata

This is a process of expulsion almost akin to parturition, and is brought about by the outward growth of the neck of the cotyledonary body. There is much that is of great interest in this subject ; and I may add that Haberlandt, in a memoir published in the *Annales du Jardin Botanique de Buitenzorg* for 1894, gives the results of an elaborate study of the viviparous process in this and other genera of mangroves. The same analogy seems also to have

presented itself to him, but only in connection with the means employed in some of the genera, as with Bruguiera, for conveying nourishment to the growing embryo. He remarks that he was involuntarily reminded by these structures of the chorion-tufts and lobes in the placenta of mammals, and that such structures in the mammal are functionally nothing more than true *haustoria* as found in the viviparous mangroves.

When studying the germination of the American and Asiatic Rhizophoras in Fiji, I observed that the neck of the cotyledonary body did not begin to form, nor the inclosed plumular bud to show signs of differentiation, until the hypocotyl had protruded about 4½ inches with R. mangle, and between 6 and 7 inches with R. mucronata. The neck of the cotyledonary body then proceeds to grow in length, pushing before it the plumular end of the embryo-seedling, which it surrounds as a sheath. This operation continues until the hypocotyl has acquired a length of about seven inches with R. mangle, and about nine inches with R. mucronata, when the neck begins to protrude outside the fruit. The cotyledonary neck proceeds with its growth, and by the time the seedling is ready to fall from the tree it protrudes about an inch from the fruit-shell, having carried the growing plumular bud with it. The plumular end of the seedling has been now more or less expelled from the fruit-cavity, and the connection between the suspended seedling and the fruit now alone depends on a slight bond between the base of the plumule and the inner margin of the cotyledonary neck, as indicated by a cross in the figures given in the plate. The union is soon broken and the seedling falls.

Whether there is anything more than an analogy between the expulsion of a Rhizophora seedling and the birth of a mammal seems most unlikely; but the process is at all events a very remarkable one.

The means of dispersal of the genus Rhizophora

My experiments and observations were for the most part made on the Asiatic and American species in Fiji; but I enjoyed the opportunity of confirming some important points on the coast of Ecuador. We can only look to the currents for the explanation of the capacity of the genus to cross tracts of ocean; but, given this capacity, there is much that is difficult to understand in the distribution of the genus and of a species like Rhizophora mangle; and it is probable that we shall have to look behind the means of

dispersal to a distant age in the distribution of shore-plants of the mangrove type.

When Schimper published his work on the Indo-Malayan strand flora in 1891, but little was known of the duration of the floating capacity of Rhizophora seedlings (p. 166). In giving the results of my investigations I am merely describing the agencies of dispersal at present in operation. Such agencies have their limitations, and we may, perhaps, be thus able to explain why Rhizophora is restricted in the Pacific islands to the archipelagoes of the Western Pacific ; but many serious objections would at once present themselves if we regarded the occurrence of the genus in America, as well as in Asia and Africa, as a matter depending on capacities and means of dispersal.

The fruits of Rhizophora, as they display themselves before the protrusion of the germinating seed, have no buoyancy, and the germinating fruits until the hypocotyl has protruded for some inches (6 inches in the case of R. mangle) also sink in sea-water. With a further increase in the length of the hypocotyl, the germinating fruit acquires buoyancy ; and when the seedling, usually 10 or 11 inches in length, becomes detached from the fruit on the tree and falls into the sea, it floats readily in 95 per cent. of the cases. Such seedlings occur very commonly in the floating drift of the estuaries and out at sea both in Fiji and in Ecuador.

Out of five seedlings of the Asiatic species, Rhizophora mucronata, that had fallen naturally from the tree, three were afloat and healthy after eighty-seven days' immersion in sea-water. Out of twenty seedlings of the American mangrove, Rhizophora mangle, sixteen floated after ninety days and four were afloat and healthy after one hundred and twenty days, the greater number sinking during the fourth month. These results indicate considerable powers of buoyancy, and go to show that extensive tracts of ocean could be traversed by the floating seedling.

It should, however, be observed that not all the full-sized seedlings float. With Rhizophora mangle about 5 per cent. sink in sea-water and from 20 to 50 per cent. sink in fresh-water ; whilst with R. mucronata the proportion of non-buoyant seedlings is rather greater. There would thus appear to be a rather nice adjustment of the specific weight of the seedlings to the density of sea-water. Generally speaking, they may be seen floating vertically or steeply inclined in the fresh-water of estuaries and horizontally in the sea. With the buoyant seedlings of Rhizophora mucronata, as a rule, about 90 per cent. float horizontally in sea-water, and about 70 per

cent. float vertically or steeply inclined in fresh-water. The same general rule applies to R. mangle, whether in the rivers and seas of Fiji or in those of Ecuador. In those cases where the seedling drops prematurely on account either of storms and floods or of the depredations of a grub that frequently attacks the fruit, this rule would not apply. One may frequently notice in Fiji after heavy weather that seedlings detached prematurely, and often carrying the fruit, are floating in numbers horizontally in the rivers. In a few days, as a rule, the fruit-case becomes detached and sinks.

It may be remarked that the horizontal position is much better adapted for the safety of the seedling in transport than the vertical position. In the last case the plumule, which protrudes above the water, would be unable, as indicated in my experiments, to withstand the scorching rays of the sun in a smooth sea; whereas in the horizontal position, which the seedlings assume in sea-water, the plumule is more or less completely submerged, and the risk of withering in the sun is very much less. The Rhizophora seedlings would certainly have little chance of crossing in safety a large tract of sea, if they floated, as they do in river-water, with the plumule exposed above the surface. It is not unlikely that the comparatively restricted area occupied by Rhizophora conjugata may be due to the attitude its seedlings assume when floating in sea-water.

The stranded seedlings of Rhizophora readily establish themselves for a while in very different situations; and it is by no means necessary that they should be washed ashore on a muddy coast. When half-buried amongst the heap of vegetable drift piled up on a sandy beach they are frequently to be found striking into the sand and showing their first leaves. Here they ultimately perish in the great majority of cases; but when protected long enough to reach the moist sand four or five inches below, they may give rise to a little mangrove colony. When caught in a fissure in the bare reef-flats these plantlets are sometimes able to establish themselves. Rhizophora seedlings would, however, require a coast prepared by them by the work of ages before they could form extensive swamps. It is, therefore, not surprising that Prof. Penzig found no evidence of mangrove-settlements on the shores of Krakatoa fourteen years after the eruption.

Yet suited as Rhizophora seedlings are for crossing tracts of sea, I regard them as quite unfitted for being transported by the currents unharmed across an ocean. The plumular bud is insufficiently protected for such a long voyage of many months, and perhaps of years. Though the horizontal position of the seedling would secure

the plumule against being scorched in the sun, it increases considerably the risk of injury from direct impact.

As bearing on their capacity for dispersal in other fashions, it may be remarked that Rhizophora seedlings can withstand long drying. Five which had been kept dry for nine weeks, after having been found stranded on a beach, were planted in the mud of a mangrove-swamp. In a fortnight two of them were developing the first leaves and throwing out roots. As long as they are protected by a covering of vegetable *débris* and sand, the stranded seedlings might retain their vitality for months.

Bruguiera rheedii (Blume)

This species is reduced in Hooker's *Flora of British India* to Bruguiera gymnorhiza (Lam.), and thus viewed it has a very wide range in the Old World, corresponding very much to that of Rhizophora mucronata, namely, tropical East Africa, tropical East Asia to the Liukiu Islands, the Indian Archipelago, New Guinea, tropical Australia, and Western Polynesia, as in New Caledonia, Fiji, Tonga, and Samoa. There are four or five species of the genus, but all are confined to the Eastern Hemisphere, none occurring in America.

As with the species of Rhizophora, this plant is indebted for its present dispersal to the floating seedling, which, however, often falls from the tree whilst still attached to the fruit, but is generally freed in a day or two. The seedlings float for a long time in sea-water. I kept one of them afloat for 117 days, when it was quite sound and healthy. They appear to be better fitted than the species of Rhizophora for the "rough-and-tumble" of ocean transport, since the plumule is much less prominent, projecting only one line (2·5 mm.) or less, whilst with the two Fijian species of Rhizophora the plumule measures from seven to twelve lines (18 to 30 mm.). In the latter part of the year they are to be found in abundance in the floating drift of rivers, and there they readily develop the first leaves and roots. They are also frequent in the sea off the coasts, and they are stranded in large numbers on the beaches, where they readily strike into the sand when partially buried amongst the vegetable drift.

The empty flowers and the germinated fruits containing the cotyledons are very common in floating drift. They look much alike, but the flowers are much smaller and possess the long style,

whilst the fruits contain the cotyledons at the bottom of the seed-cavity.

As with Rhizophora, there is a rather curious adjustment of the buoyancy of the seedling to the density of sea-water. About 75 per cent. of those afloat in the fresh-water of rivers assume the vertical position, the plumular end protruding between two and five lines (5 to 12 mm.) above the surface, while the remainder float horizontally or nearly so. In sea-water about 50 per cent. float either vertically or steeply inclined, and the other half float horizontally.

With regard to the times of flowering and fruiting, it may be remarked that the trees are mostly in flower during the hot months from November to February, and that the fruiting is in active operation in the latter half of March. The floating seedlings occur in abundance in the river-drift at the end of the year, a circumstance which corresponds with the fact that a period of six months passes between the fertilisation of the ovule and the fall of the seedling into the water.

Fertilisation, or, more correctly speaking, the discharge of the pollen, takes place after the opening of the flower, and not before, as in the case of the species of Rhizophora. The flower-bud is at first erect, but subsequently it begins to bend downwards, and ultimately it hangs more or less vertically. The provision to secure fertilisation under these circumstances is rather curious. Without some such contrivance as is below described, the pollen would merely fall out of the flower. Each petal has its sides rolled or folded inwards so as to completely inclose two stamens. In the bud the folded petals are white and flexible, but as the flower expands they redden and become dry and elastic, and are only prevented from flying open with a spring by the interlocking of the hairy tips of their lobes. Whilst the folded petals are becoming stiff and elastic during the opening of the flower, the inclosed stamens are at the same time preparing themselves for their function. The anthers are dehiscing and the filaments are acquiring elasticity. All is now ready, and a slight shake or a touch puts the mechanism into action. The petals unfold themselves with a spring, and the stamens thus suddenly exposed and released fly forward, and a little shower of pollen is thrown towards the centre of the flower. This process is accomplished in ordinary fine weather during the first twenty-four or thirty-six hours after the expansion of the flower. When the opening occurs in the early morning, half of the stamens will be found released in the evening and the

rest on the following day. During the next day or two the petals and the stamens fall out of the flower. In wet weather, the petals never acquire elasticity, and in consequence do not unfold. In this case pollenisation is never effected, and the folded petals soon fall to the ground, carrying the stamens within them. Cross-fertilisation would be much more likely to occur with species of Bruguiera (if, as is probable, the same process of pollenisation is usually followed) than with species of Rhizophora, since the stamens are securely inclosed in the petals for some hours after the expansion of the flower.

Nearly eight weeks pass between the date of fertilisation and the commencement of germination. This is somewhat similar to the period given for Rhizophora mangle, namely, nine weeks, and it obviously leaves little or no time for any stage of quiescence or dormant vitality in the case of the seed. The changes which the fruit undergoes in this interval are a considerable increase in girth and a thickening of the calycine walls, together with a contraction of the mouth of the tube. However, I found no method sufficiently accurate for recording the rate of increase of the fruit.

It is known that germination is in progress when the end of the hypocotyl begins to lift up the lining membrane at the bottom of the calycine tube (see Figs. 21 to 26). The floor of the tube begins to bulge up, but since this cannot be well seen at first, a better index is afforded in the elevation of the style which accompanies it. The top of the style preserves previous to this time a constant level with regard to the tips of the calycine teeth. But this does not indicate the actual beginning of germination. As shown in Fig. 21, the seed lies about two and a half lines (6 mm.) below the floor of the calycine tube, and the tip of the hypocotyl has to penetrate the intervening tissues before it can push up the lining membrane and raise the style. Judging from the subsequent rate of growth, seven or eight days at least, and perhaps as much as two weeks, are requisite for this purpose. It is not necessary to give further details here, and it may be at once stated that the average of numerous observations on the length of the interval between fertilisation and the elevation of the style was sixty-four days, the range being fifty-nine to sixty-nine. After deducting ten days for the time occupied for the radicle in reaching the floor of the calycine tube (see Figs. 22 and 23), we obtain, as already remarked, nearly eight weeks as the time elapsing between fertilisation and germination.

The radicle or hypocotyl, therefore, in the first stage of

germination pierces the tissues above it and reaches the floor of the calycine tube. It does not, however, pierce the lining membrane of the tube but pushes it upward until it ruptures about 4 millimetres below the base of the style which is carried up with it. Thus a kind of cap is formed, as shown in Fig. 24, which does not fall off from the end of the hypocotyl until it has protruded rather more than an inch. The hypocotyl attains a length varying between 5 and 11 inches, the average being about 8 inches.

The whole period may be thus divided up :—

(1) Period between fertilisation and germination	$7\frac{1}{2}$	weeks.
(2) Period between the beginning of germination and the protrusion of the point of the hypocotyl at the floor of the calycine tube	$1\frac{1}{2}$	"
(3) Period occupied in the growth of the hypocotyl 8 inches outside the fruit and terminating in the fall of the seedling . . .	18	"
Total	27	weeks.

The total period of twenty-seven weeks between fertilisation and the fall of the seedling is thus six weeks shorter than that estimated for Rhizophora mangle. On comparing the two tables it will be seen that the difference mainly lies in the length of the second period, namely, that between the commencement of germination and the protrusion of the hypocotyl from the fruit. With Rhizophora mangle the fruit grows considerably in length during this period of the germinating process. On the other hand with Bruguiera rheedii there is, during this period, practically no increase in the length of the fruit, and the radicle has only to penetrate the tissues, $2\frac{1}{2}$ lines in thickness, between the seed and the floor of the calycine tube.

In the mode of separation of the seedling there are very marked differences between this species of Bruguiera and the species of Rhizophora. With Bruguiera rheedii the four small cotyledons, which are united at the base, are, however, left behind at the bottom of the seed-cavity, when the seedling is detached. But there is no expulsion of the seedling, the connection being ultimately severed at the contracted base of the cotyledons inside the fruit. When the seedling is full-sized the nutritive supply begins to fail, and in consequence the pressure of the sides of the

fruit on the inclosed plumular end of the seedling becomes slacker, the union with the cotyledons becomes weaker, and the connection of the fruit with its peduncle at the basal joint becomes slighter. Usually the fruit falls before the seedling is ready to drop out, and the connection is severed after a few days' flotation in the water; but sometimes the union between the seedling and fruit is weaker than that between the fruit and its peduncle, and in that case the seedling falls and leaves the fruit containing the cotyledons on the tree. The whole process of separation is much simpler than with species of Rhizophora. Here it is mainly a matter of the failure of the nutritive supply, whilst with Rhizophora it is almost a process of parturition.

Haberlandt, in the memoir before quoted, describes quite a different mode of detachment in the case of Bruguiera eriopetala. Here the seedling falls normally whilst still attached to the fruit, and the separation is subsequently effected by the expansion of the mouth of the calyx-tube due to the swelling of the "endosperm-neck" from the entrance of water.

Summary

(1) There are four typical mangroves of the Rhizophoraceæ in Fiji, Bruguiera rheedii, Rhizophora mucronata (the Asiatic species), Rhizophora mangle (the American species), and the Selala, a seedless form intermediate between the two species of Rhizophora just named, but nearest to the Asiatic species.

(2) It is shown that the sterility of the Selala is connected with the impotent character of the pollen; and since the ovules appear capable of fertilisation this is held to indicate that cross fertilisation has not been in operation in producing the barren form.

(3) Good reasons are given for the belief that the Asiatic species of Rhizophora is the parent of the Selala, not as the result of a cross between the Asiatic and American species, but as connected with dimorphism, the Asiatic species producing two kinds of offspring, one of them with impotent pollen.

(4) In support of this view it is pointed out that there are two forms of Rhizophora mangle in Ecuador, one of which comes near the Fijian Selala, though producing seed. There could thus be no question of crossing, since but one species occurs there.

(5) The Selala reproduces itself in a vegetative fashion when growing, as it often does, in an inclined position. The parent

trunk dies and the primary branches supported by the aërial roots, remain alive and in their turn give rise to secondary branches similarly supported.

(6) Although, as a rule, only one of the four ovules of Rhizophora becomes a seed, occasionally a fruit contains more than one seed. With R. mangle in Fiji about one per cent. of the germinating fruits displayed more than one hypocotyl.

(7) As a result of a protracted series of observations in Fiji, it was established that in the case of a seedling of average length of Rhizophora mangle a period of thirty-three weeks elapsed between the date of fertilisation of the ovule and the detachment of the seedling from the tree. In the instance of R. mucronata it was placed at forty-two weeks. A period of thirty-eight weeks, or nine to ten months, is regarded as typical for the genus.

(8) It is established that normally there is no rest-period for the seed in the case of Rhizophora, the seed at once beginning to germinate on reaching maturity. In those exceptional instances, however, where there is more than one seed, it is shown that in some cases the seeds do not begin to germinate together, and that a rest-period of at least some weeks can be at times postulated for one of the seeds.

(9) An analogy exists between the process of expulsion ending in the detachment of the seedling of Rhizophora from the fruit and the process of parturition.

(10) Experiments show that Rhizophora seedlings can float unharmed in sea-water for a period of at least three or four months. Though nine-tenths or more float in sea-water, as much as a fourth or a half sink in fresh-water. As a rule they float vertically in fresh-water and horizontally in sea-water, the horizontal position safe-guarding the plumule against the risk of being withered up by the sun in a calm sea.

(11) It is shown that in the case of Bruguiera rheedii the seedlings when detached from the tree can float unharmed in sea-water for months. In their specific weight they display a similar fine adjustment to the density of sea-water, as is above described in the case of Rhizophora.

(12) With this species of Bruguiera, fertilisation takes place not in the unopened flower, as in Rhizophora, but after the flower's expansion ; and a very singular mechanism is here described which secures the completion of the process.

(13) A period of twenty-seven weeks elapses between the fecundation of the ovule and the detachment of the seedling from

the tree in the case of Bruguiera rheedi ; and it is shown that there is normally little or no room for any rest-period, and that, as with Rhizophora, the seed on reaching maturity begins to germinate.

(14) Though the seedlings of Rhizophora and Bruguiera could be transported in safety a few hundred miles across the sea, it is held that they could never cross the Pacific and reproduce the plant. That the American species of Rhizophora has reached the Western Pacific from the New World is not accepted. Rather is its present distribution regarded as representing its original wide range over much of the tropical zone.

CHAPTER XXXI

A CHAPTER ON VIVIPARY

The significance of vivipary.—The scale of germinative capacity.—A lost habit with many inland plants.—The views of Goebel.—The shrinking in the course of ages of tropical swamp areas.—The variation in the structures concerned with vivipary.—Abnormal vivipary.—Summary.

It was remarked in Chapter IX that the study of the germination of the floating seed carried us to the borderland of vivipary; and we may now observe that our study of the mangroves, Rhizophora and Bruguiera, in the previous chapter, has brought us into contact with vivipary in its most complete development in the tropical swamps of our age. There is a great gap between the two extremes, represented by the occasional germination of a seed in a capsule or in a berry on the plant, and by the elaborate process of vivipary exemplified by Rhizophora; but most of the intermediate stages can be illustrated by known examples of vivipary. There is, however, no pretension to deal with this subject here in anything but a cursory fashion; but it will, I venture to think, add completeness to a work in which germination on and off the plant has been such a frequent theme if I endeavour to connect together some of the various sets of facts known to us concerning germination from the standpoint of vivipary.

The principal argument here followed has been already outlined in Chapter IX, where I have remarked that it is possible to construct a scale of the germinative capacities of plants, presenting a continuous series beginning with the mangroves, where germination takes place on the tree, and ending with those numerous inland plants where seeds are liberated in an immature condition. It is suggested that vivipary was the rule under the

uniform climatic conditions of early geological periods, and that with the differentiation of climates that has marked the emergence of the continents the viviparous habit has been lost over much of the globe, the mangrove-swamps alone illustrating the climatic conditions once prevailing. The rest-period of the seed is regarded as an adaptation to climatic differentiation and to seasonal variation; and even the seed-stage may be broadly regarded as the price paid for adaptation on the part of the evolutionary or determining power that lies behind plant-development. When discussing the germination of Cæsalpinia in Chapter XVII, I have shown that the contraction and induration of the seed-tests appear merely as an adaptation to climatic differentiation and to seasonal variation, and that it would be quite possible by exposing the maturing seed to very warm and moist conditions to induce germination without any rest-period, as actually occurs with Rhizophora. One would then dispense altogether with the final processes of the contraction and induration of the seed-coats, as illustrated in the Leguminosæ; and the rest-stage would appear as an adaptation to secular differentiation of climate in the later epochs of the world's history.

The significance of occasional vivipary was long ago pointed out by Goebel in his *Pflanzenbiologische Schilderungen* (teil I., 117–134, Marburg, 1889), when he observed that vivipary, as displayed in the mangroves, and particularly in the Rhizophoreæ, represented the fullest expression of a habit that is only occasionally exhibited by other plants under exceptionally moist conditions. His view was that the seeds of plants living in wet places are suited in a varying degree for rapid germination, and that vivipary presents itself as the most complete development of this capacity. If I regard the views of Goebel and of Kerner aright, vivipary as normally developed in the mangrove is to be traced in a descending scale to small beginnings, the principal determining condition lying in the great difference that exists amongst plants in the readiness of the seed to germinate. In the ascending scale we would have first the detachment of the immature seed, where the embryo is often in a rudimentary state, the ripening of the seed taking place in the soil. Then would come those plants where the seeds on being detached are quite mature and are ready to germinate as soon as they fall to the ground. Then would follow the stage represented by those plants where the seeds merely begin to germinate on the plant, such as occurs more or less normally with some mangroves like Laguncularia, and abnormally with a number

of plants living in drier stations. After this come those mangroves, where, as in Avicennia, germination is completed on the tree or shrub, but the seedling at once liberates itself from the parent. Last of all there is the stage of the typical mangroves, Rhizophora and Bruguiera, where the seedling remains for months growing on the tree and hangs from the branches.

Vivipary, as above stated, presents itself as a matter of small beginnings. My own view, however, is that it is a matter of small "endings"; and that if we were to commence the scale not with the immature seed lying on the soil, but with the seedling suspended from the branches of a Rhizophora tree, we should record the various epochs in the history of vivipary throughout the plant-world. From this standpoint the occasional cases of incomplete vivipary displayed outside the mangrove-swamp represent a lost habit belonging to a primeval period when the climatic conditions were uniform over most of the earth, an age almost of eternal gloom, when the air was ever saturated with aqueous vapour, and when the sun's rays were screened off by a dense cloud-covering that enveloped the globe, an age of which the existing mangrove swamps alone afford an imperfect indication. Yet even now we can say with Schimper that "dense and frequently repeated cloudiness apparently represents the most essential climatic condition for the occurrence of mangrove in the tropics" (*Plant Geography*, p. 409).

But, to return to the subject immediately under consideration, if my view is correct we ought to find indications of the lost habit in the anomalous structure of the seeds of some inland plants; and, indeed, it is shown in Note 50 that this view can be taken of the singular structure of the seeds of the Myrtaceous genera, Barringtonia and Careya, and of the genera of some other orders, and can be extended by implication to several other plants possessing similar seed-structures.

With regard to the subject generally, it may be remarked that although normal vivipary is mainly restricted to the plants of a mangrove swamp, by no means all mangrove plants are typically viviparous. This habit in its most complex form is exhibited as a rule by plants with firm, somewhat fleshy, usually one-seeded, indehiscent fruits, such as we find with Rhizophora and Bruguiera; but plants with follicular fruits, such as occur with Ægiceras, may also display it in a fashion nearly as complex. Generally speaking, however, plants with hard, dry fruits, such as are owned by Excæcaria, Heritiera, and Lumnitzera, are non-viviparous, though

to all appearances quite at home in a mangrove-swamp. Others again, like Carapa, Laguncularia, and Nipa, whilst displaying vivipary in a varying degree, in some cases as a general rule, in others only occasionally, exhibit no special structures connected with it. This point is well brought out by Schimper in his work on the Indo-Malayan strand-flora (p. 43), and no further mention need be made of it here.

The structures connected with vivipary vary greatly in their degree of specialisation. At the one end of the scale we have highly complex structures, such as are described in the preceding chapter. At the other end we have those cases of occasional germination on the parent plant where there is seemingly no special structure of any sort. That the complex arrangements concerned with the vivipary of Rhizophora, Bruguiera, Ægiceras, and Avicennia are adaptations is argued by Haberlandt and Schimper, both of whom devoted much attention to the study of these plants. This is seemingly indicated by the circumstance that complex structures concerned with vivipary are found in plants so divergent in their characters (the four genera above-named representing three orders, Rhizophoreæ, Myrsinaceæ, and Verbenaceæ) that they only possess their stations in common. It does not, however, follow that all mangroves that exhibit a complex form of vivipary are of the same antiquity. I should be inclined to regard those of the Rhizophoreæ as the more primitive types, whilst it is possible that plants of other orders, though ancient denizens of a mangrove-swamp, may be more recent intruders into the mangrove-formation after the differentiation of a dry-land flora.

Of particular interest in this connection are the cases of abnormal vivipary, or of "precocious germination," that have been recorded from time to time respecting a number of plants not denizens of a mangrove swamp, none of which would appear, according to Schimper's views, to present anything of the nature of an adaptation. Goebel mentions a number of instances, such as that of wheat-grains germinating on the stalk in a wet summer, and that of Dryobalanops camphora, the Borneo camphor-tree, when during a prolonged wet season in Java the seed germinates in the fruit on the parent tree. Amongst other examples he cites the Cacti, Epilobium, Agrostemma, and Juncus, the last case coming also under my observation in a wet season in England. One may here notice the instance of Dracæna, of which Mr. Hemsley, in April, 1902, exhibited at a meeting of the Linnean Society of London a

specimen showing the seeds germinating in the berries on the plant.

Several cases of this kind came under my notice in Fiji. Pulpy fruits rather favour the precocious germination of seeds. Thus I sometimes found the seeds germinating in the Mandarin orange and in the Papaw fruit (Papaya) shortly after they had been gathered. But more interesting examples were displayed in those instances where the seed was found germinating on the plant. When the Convolvulaceæ grew in wet situations, as on the borders of a mangrove swamp, the seeds were sometimes observed germinating in the capsule. This came under my notice with Ipomea glaberrima (Boj.) and with I. peltata, more particularly in wet weather. With some other plants, like Hibiscus diversifolius, that grow in wet places, this at times occurs. A species of Croton, employed as a support for the Vanilla plants in a plantation near Suva, displayed seeds germinating on the plant. I was informed that the seeds of the common cultivated Luffa (L. cylindrica) growing in a garden on Vanua Levu sometimes germinated in the fruit still attached to the parent. It is possible that the seeds of the parasitical genus, Myrmecodia, may occasionally germinate on the plant, since I found them germinating inside some of the small berries that had been lying forgotten within a newspaper for a fortnight.

Perhaps the most curious case of abnormal vivipary observed by me in Fiji was that concerned with the Coco-nut palm. Though not known to many residents in the island, this habit was described to me by Mr. Matthew Simpson, a planter on Vanua Levu, who told me that he had noticed nuts germinating on the tree in unusually dry seasons. Coco-nut palms displaying the nuts germinating on the tree came under my observation near Bale-bale, Savu-Savu Bay. In these cases the mature fruit, instead of falling, remains attached and dries on the stalk. In one case the seedling was about eighteen inches high. This seems to be what takes place normally according to Blume with Nipa fruticans, the swamp palm of Indo-Malaya. Goebel quotes this author to the effect that the fruits are not separated from the head before germination is so far advanced that sea-water can no longer injure the seedling. The fruits, we are told, may remain for years attached in a state of incomplete germination.

Summary

The scale of germinative capacity, that begins with the seedling hanging from the branches of a mangrove like Rhizophora and

ends with the detached immature seeds of many inland plants that only germinate after lying for some time in the soil, is regarded as supplying a record of the various epochs in the history of vivipary throughout the plant-world. In the occasional cases of incomplete vivipary occurring among inland plants and in the singular structure presented by the seeds of certain genera of the Myrtaceæ and other orders we perceive indications of a lost viviparous habit belonging to a primeval period when vivipary was the exception and not the rule, an age when the same climatic conditions prevailed over much of the globe. At such a period the sun's rays were screened off by a dense cloud-covering that enveloped the earth, and the atmosphere was ever charged with moisture. With the differentiation of climate that has marked the emergence of the continents during the secular drying of the earth, the viviparous habit has been alone retained within the confines of the mangrove-swamp, where the conditions once almost universal now survive; and as an adaptation to the differentiation of climate and to the resulting seasonal variation the rest-period of the seed has been developed.

CHAPTER XXXII

THE WEST COAST OF SOUTH AMERICA

The littoral floras of the West Coast of South America.—The Convolvulus soldanella zone of Southern Chile.—The plantless or desert zone of Northern Chile.—The Sesuvium zone of Peru.—The Mangrove zone of Ecuador and Colombia.—The two varieties of Rhizophora mangle, the "mangle chico" and the "mangle grande."—The floating vegetable drift of the Guayaquil River.—The Humboldt current and the climate of the West Coast of South America.—The advance northward of the arid climatic conditions of the Peruvian sea-border.—The retreat of the mangroves.—Evidence of ancient coral reefs on the coast of Peru.—The shore plants and stranded seed-drift of the Panama Isthmus.—Summary.

My acquaintance with the strand-flora of the west coast of South America began at Corral, the port of Valdivia, in Southern Chile in lat. 40° S., and terminated at the mouth of the Guayaquil River, in Ecuador, about 2° south of the equator. During the period December 23, 1903, to March 17, 1904, I examined the coast plants at sixteen localities in this region, which covers 38 degrees of latitude and thus measures about 2,300 miles. Travelling in a steamer to Callao that was trading on the coast I had opportunities of staying for periods ranging from half a day to a couple of days at a considerable number of places; and a week spent at Valparaiso gave me a good opportunity of examining the beaches north and south of it. At Lima I spent some weeks, and from that centre examined the shore-plants at Callao, Ancon, and Chancay to the northward. North of this I had not the same opportunities, until we passed the Peruvian and Ecuadorian boundary; but from a visit to the shore at Paita, from the general look of the country in places as we coasted along, and from information derived from other sources, I was able to obtain a fair general idea of the prevailing character of the beach plants. After my previous experience to the southward, one could fairly gauge

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the character of the beach-flora from the appearance of the land behind. In the Gulf of Guayaquil and in the vicinity of the city of that name I spent about three weeks in the investigation of the coast flora.

If it were not for the interposition of the great rainless deserts of Northern Chile and for the scantily vegetated, scantily watered and semi-sterile condition of almost the whole coast of Peru, the botanist would be presented with a splendid opportunity of studying the distribution of shore-plants along a meridian stretching through some fifty degrees of latitude from Patagonia to Ecuador. As it is, drought and sterility in one form and another reign over about half of this great stretch of continental coast. This is reflected in the beach-flora; and though the observer will often have his interest attracted by the wonderful climatic anomalies arising from the presence on the coast of the cold Humboldt current, to which the sea-border of North Chile owes its desolation and the coast of Peru its semi-sterility, yet for a long time he will feel as if Nature had hardly dealt fairly with him.

Along the sea-border corresponding to the deserts of North Chile there would seem to be practically no plants growing on the beaches, except here and there where some stray plant from the saline districts inland intrudes on the coast. Along the whole sea-border of Peru from Arica north to Tumbez on the borders of Ecuador, the coast-districts, though more or less rainless, receive the benefit of the drizzly garuas and sea-fogs, and the sterility of the land immediately backing the beaches is much less pronounced than with the sea-border corresponding to the deserts of Northern Chile. This difference shows itself in a peculiar type of littoral vegetation, a strand-flora that is very scanty but one where on the beaches Sesuvium prevails. North of Tumbez the mangrove-formation predominates along the sea-borders of Ecuador and Colombia to Panama, excepting on a stretch of sterile coast extending north from the Gulf of Guayaquil to the equator.

Though in one sense the botanical observer will be disappointed with the littoral floras of the west coast of South America, in another sense when he remarks the manner in which the coast-vegetation reflects the abrupt changes in the prevailing climatic conditions he will be fascinated by the interesting problems presented to him. We are accustomed to connect a tropical coast with mangroves, coral-reefs, and beaches of calcareous sand supporting a luxuriant littoral flora. Climatic conditions banish all

these from the tropical west coast of South America until within four degrees of the equator, and then with startling suddenness the dominion of the mangrove begins, the neighbouring hills commence to be clothed with tropical jungle, and the climate is completely changed. Mr. John Ball, who sailed along this coast about twenty years ago, referring to this remarkable phenomenon on the borders of Peru and Ecuador, remarks that no such abrupt and complete change both in climate and vegetation is known elsewhere in the world, and he adds that few parts of the American coast better deserve careful examination (*Naturalist in South America*). This subject has since been discussed at length by Dr. Wolff in his "Geografia y Geologica del Ecuador," and by Baron von Eggers in a paper to be subsequently quoted, two very competent observers, but the latter considers that the subject still requires a systematic investigation, and suggests that an observing station should be established on this coast by the combined meteorological societies of Europe. A sojourn of more than a week in the swamps at Puerto Bolivar, a few miles from Tumbez, enables me to appreciate the nature of the problem, and to throw a little light on the line of investigation required.

But to return to the general subject of the littoral floras of the west coast of South America, I may say that beginning with the island of Chiloe in lat. 42° S., this coast may be divided into four zones.

(1) The Convolvulus soldanella zone of Southern Chile, which extends as far north as Coquimbo about 30° S. lat.

(2) The Plantless or Desert zone stretching north to the vicinity of Arica in lat. 18° 30′, and corresponding to the coast of Northern Chile.

(3) The Sesuvium zone, extending north from Arica to the 4th parallel of south latitude in the vicinity of Tumbez, a sea-border of semi-sterility that comprises the entire coast of Peru.

(4) The Mangrove zone, stretching from Tumbez, on the frontiers of Ecuador, to the equator and on to Central America, but interrupted at first by a strip of sterility on the coast extending from the Gulf of Guayaquil to the borders of Colombia, or, strictly speaking, to the equator.

The Convolvulus soldanella Zone (Southern Chile).

This zone, which answers to the coast of Southern Chile, from Chiloe as far north as Coquimbo, corresponds to watered and

vegetated inland regions, in which, however, the amount of rain and the degree of fertility decreases from south to north, that is to say, as we approach the desert regions. Here we find none of the dry beaches that prevail for twenty-five degrees of latitude north of Coquimbo. When we scoop with our hands to a depth of three or four inches in the sand we find it relatively cool and more or less moist, as in an English beach. In a hot summer's day on a Valparaiso beach we should find that the temperature of the sand at the surface (half-inch deep) was about 112° F., and at a depth of four inches about 80°. This would be above the average for the zone, which would be probably near the typical summer-temperature of an English beach, namely, 102° at the surface and 77° four inches down. This subject of beach temperature is discussed in Note 70.

Plants typical of the beaches of this zone, and evidently occurring over the length of it, are Convolvulus soldanella, Nolana (paradoxa?); Polygonum maritimum, Salsola Kali, and Selliera radicans. Nolana is a Chilian and Peruvian genus. This beach plant, which is especially abundant on the beaches near Coronel and at Bahia San Vincente, has the creeping habit of its associate, the Convolvulus. However, it possesses seeds, or rather seed-vessels, of more limited buoyancy; and it is shown in Note 71 that prolonged drying is needed for effective dispersal by currents over great distances. This beach species of Nolana has narrowly escaped being a widely-spread littoral plant; whereas it is now restricted to the Chilian beach flora. Selliera radicans, a little creeping Lobeliaceous plant, growing under the shade of tall clumps of Juncus at the edge of the beach or in wet places where springs ooze out in the sand, is a very interesting species that occurs also on the other side of the Pacific in Australasia. Of the mode of dispersal of its small seeds I know nothing, as the fruits were not ripe at the time of my visit; but I would suggest that some resident botanist should investigate this important point. I found it at Corral and at Coquimbo; and Gay speaks of it as growing on wet coast places from Chiloe to Coquimbo, a range of $12\frac{1}{2}°$ of latitude.

It is probable that all the shore-plants of this zone extend south to Chiloe in latitude 42° S.; and it is likely that some of them reach towards the Straits of Magellan. I did not find any of them within the Straits on the beaches in the vicinity of Punta Arenas, where, however, I noticed the three plants recorded by Ball, namely, Armeria maritima, var. andina; Senecio candidans,

also found in the Falkland Islands; and Plantago maritima; besides a Chenopodiaceous plant not in fruit. The Plantago has no capacity for dispersal by currents, and probably none of the other plants are thus dispersed. I formed the opinion when in the Straits that the beach plants on the Pacific and Atlantic coasts of Patagonia could have but little communication by the currents, and that they are in this respect quite cut off from each other. A botanist who investigates the strand-flora of Patagonia and Tierra del Fuego in connection with the littoral plants of the opposite coasts ought, if he has not already done so, to obtain some very interesting results from the standpoint of plant-dispersal.

The northern limit of the plants of this zone near Coquimbo, in lat. 30° S., is not determined by the change in climatic conditions that goes normally with decrease in latitude, but by the vicinity of the great deserts of Northern Chile, the aridity extending to the beaches.

Amongst the other plants occurring generally in the Convolvulus soldanella zone of Southern Chile, species of Salicornia and Samolus are to be observed in wet places. On the beaches near Valparaiso and in the vicinity of Talcahuano there thrives a species of Franseria, a Composite plant possessing prickly fruits well suited for conveyance in bird's plumage, but not adapted, as shown in Note 71, for dispersal by currents. Mesembryanthemum is a typical beach-plant at Coquimbo, and an intruder from the adjoining hill-slopes at Valparaiso. Raphanus, seemingly R. maritimus, occurs in places, but apparently only as an intruder from the cultivated districts behind the beaches. One or two species of Euphorbia are not uncommon. A few small trees or bushes of Acacia farnesiana grow typically on the beach at Coronel and in neighbouring sandy tracts at Talcahuano, though the plant, as Gay observes, has been introduced. Sophora tetraptera, found also in New Zealand, and one of the most interesting plants of the Antarctic flora, thrives as a small tree on the hill slopes overlooking the harbour of Corral, becoming bushy where in places it intrudes on the beaches, and fruiting there as freely as on the slopes above. It was by testing the buoyancy of the seeds of this plant that I was led to the discovery of its mode of dispersal by the currents (I am indebted to Mr. Holland for the specific determination of the fruits sent by me to the Kew Museum). Other shore-plants, of course, occur in this zone; but I have gone far enough to illustrate the subject. Of the numerous occasional intruders from the neighbouring inland

districts, frequently Compositæ, I say nothing. The results of my observations on the floating power of the seeds and seed-vessels of some of the shore-plants of this zone are given in Note 71.

Stranded seeds and fruits that belong to the proper beach-drift are not easily found on the beaches of Southern Chile, as they are often buried in rubbish. Those most characteristic are seeds of Convolvulus soldanella and drupes of Nolana (paradoxa?), both typical beach-plants of the zone. Portions of Salsola Kali bearing mature fruits, as described in Note 17, are also frequent. Seeds of Sophora tetraptera were found on the beach of Bahia San Vincente, whither they must have been brought by the Humboldt Current from the south, as I did not observe the tree in the vicinity. On this beach, as well as at Valparaiso, the prickly fruits of Franseria were abundant in the drift, doubtless derived from the plants growing on the same beaches. In addition we get as frequent components of the beach-drift materials that mark the white man's presence over much of the globe. Corks are widely distributed over the beaches of the world; but on no coast have I found them more numerous than on the Valparaiso beaches. Here we find Medicago fruits, the empty stones of the cherry, the plum, and the peach, empty filberts and other materials, all of which I have gathered on the shores of the Straits of Messina and on English beaches. Amongst this medley we find also Casuarina cones and fruits of Eucalyptus. Then we find special indications of the New World in the pea-nut (Arachis hypogæa) and in the abundant seeds of a huge pumpkin (Cucurbita), which is a favourite food with the Chilian indigenes. These seeds are cited as an example of futile buoyancy in Chapter XIII.

THE PLANTLESS OR DESERT ZONE (NORTHERN CHILE).

This zone of the coast, which stretches north for some 700 miles from Coquimbo to near Arica (30°—18°30′ S. lat.), corresponds to the great desert region of North Chile. On the beaches of Antofagasta, Tocopilla, and Iquique, which are situated in the midst of this zone, I found no plants. This rainless sea border of barren mountains, presenting to the eye of the traveller from the deck of a passing steamer nothing but rock and sand, must be one of the most desolate coasts on our globe. It is therefore not a matter for surprise that the beaches are of dry loose sand in which the hand fails to find on scooping below the surface that refreshing coolness which is the character of beaches in all latitudes where the land is

vegetated and a subsoil drainage seaward exists. Under ordinary conditions the sensation of moisture in the sand a few inches down is not produced by the mere proximity of the sea. On the Antofagasta and Iquique beaches the temperature in the heat of the day of the surface half inch ranged from 120° to 130° F., whilst four inches down it was 95° to 100°, and no moisture was found by scooping five or six inches down. On the Taltal beach, which lies towards the southern end of the desert region, I noticed, besides a few plants of Suæda fruticosa, two other species of the orders Santalaceæ and Nolanaceæ, evidently intruders from the inland regions. Where the zone of extreme aridity terminates at the north between Pisagua and Arica a few bushes are to be seen on the hill-slopes behind the beaches.

Very little seed-drift came under my notice on the beaches of the desert zone. Here and there I found a few Medicago pods and some seeds of the large pumpkin above noticed, but that was all. This is due as a rule to the seed-drift being masked by an enormous amount of rubbish, mostly brought from the south by the Humboldt Current. My walk for five miles along the beaches immediately north of Antofagasta gave me an experience in the way of stranded drift such as I have never met with on the beaches of any other region. All the dead bodies of the Chilian coast to the southward seem to have been stranded in the bend of Moreno Bay, on the shore of which Antofagasta lies ; and the air was tainted with decaying flesh, the past being mixed up with the present in a most unrefreshing fashion. Besides carcases of sea-lions, six feet in length, sharks, dog-fish, and fish of many sorts, some of them dried up, others in a state of putrefaction, there were dead penguins, dead pelicans, dead sea-birds of other kinds, the bodies of horses, cattle, dogs, &c., all preyed upon by the numerous vultures and skuas, and in some localities by hungry-looking dogs of large size that took no notice of me as they slunk along. The past was represented by great quantities of bones that lay bleaching on the sand, with here and there a vertebra of a whale, making in all quite a varied osteological collection. But this was not all. Carcases of all sorts were drifting towards the beach. Here a vulture, there a skua, there again a dog stood just beyond the tide-wash looking keenly seaward ; and by following the direction of their gaze one could see that each had marked down a carcase slowly drifting in. Now and then they would make a dash, scarcely waiting for the new arrival to be washed up by the waves. But there was no competition, since there was enough for all.

Under such conditions my investigation into the seed-drift was out of the question; but I saw what would be considered by some as more interesting, namely, the dead of many latitudes piled up on the beach by the Humboldt Current.

THE SESUVIUM ZONE (THE PERUVIAN COAST).

This zone, which comprises the whole Peruvian sea-border from Arica in 18°30′ S. to the vicinity of Tumbez in about 3°30′ S., usually possesses in its scanty littoral flora one or two species of Sesuvium, and in some places Sesuvium alone occurs on the beach. The beaches here do not line a region of almost complete aridity, as in the coast corresponding to the great desert region of North Chile. Though here also scarcely any rain falls, the sea-border receives the benefit of the "garuas" or drizzling sea-fogs; whilst the region immediately behind the coast may either be desert or semi-sterile during much of the year, or may be scantily vegetated, or, as along the river-valleys, may display a vegetation more fitting to the latitude. The general aspect, however, of the coast of Peru is one of aridity; but there are probably few beaches where a certain amount of subsoil drainage from the land sea-ward does not exist. This is well exhibited at Ancon, north of Callao, where in the most unlikely situations water is reached by digging wells; but in spite of this the Sesuvium alone grows on the beach. The beaches examined by me in the heat of the day in February, as at Mollendo and Ancon, had much the same surface-temperature noticed in the preceding month on the beaches of North Chile, namely, 120° to 130° F., and in one place 135°; whilst at a depth of four inches the sand was rather cooler, and instead of being between 95° and 100°, as on the Antofagasta and Iquique beaches, it was here usually only about 90°. But it was only occasionally that the sand felt at all moist at a depth of five or six inches; and in this zone, therefore, only a few shore plants of a peculiar type could be expected to find a station on the beaches, excepting, of course, those localities where low marshy districts or lagoons lie behind the beach.

The beach plants of the coast of Peru as observed by me though usually scanty, presented two types according to the character of the district bordering the beach. I make no mention here of those local plants, often belonging to the Compositæ, that as at Callao and Arica descend the valleys to the beaches, or to those numerous introduced plants that accompany cultivation,

such as we find at Arica. In those coast localities, as at Arica Callao, and Chancay, where salt-water pools or brackish lagoon lie behind the beach, or where a stream or a river empties into th sea, Sesuvium portulacastrum, Heliotropium curassavicum, and Salicornia are to be generally noticed, and, as at Callao, Batis mari tima may also abound. On the Chancay coast, about 30 mile north of Callao, there lies inside the shingle-beach a large shallow lagoon of brackish water (spec. gr. 1·012) with extensive mudd marginal flats, the temperature of the water at the edge being a mid-day on Feb. 3rd, 90° F. In the water flourished Ruppia maritima, which was also exposed in dead, dry, matted masses on the bordering mud-flats. On these mud-flats grew Sesuvium portulacastrum, which near the water's edge was associated with small species of Salicornia, whilst further away from the water i was accompanied by Heliotropium curassavicum.

But the most typical beach-flora of the Peruvian coast is such as we find on the dry beaches skirting the base of sand-covered o barren hill-slopes such as occur at Mollendo, Ancon, and Paita As at Ancon, sand-covered hills and plains may extend mile inland, displaying here and there lines of shifting sand-mounds o "medanos." On such beaches we may often find only a solitary plant, a species of Sesuvium which seems to differ only in its larger flowers, its much larger leaves (2 inches long), and its stout stems, of the thickness of the little finger, from the ordinary Sesuvium portulacastrum. This seems to be the only plant that can make its home on such beaches. At Mollendo, where there are signs of desiccated pools behind the beach which are occasion-ally filled with sea-water, the vegetation was of an intermediate character and more abundant; and here grew Sesuvium portula-castrum, a tall Salicornia, and Suæda fruticosa; whilst the commonest plant was a prostrate Nolanaceous species with a handsome purplish flower.

Excepting with the fruits of Batis maritima, and perhaps the buoyant joints of Salicornia, scarcely any of the prevailing shore-plants of the coast of Peru possess a capacity for dispersal by currents. In this zone I rarely found any seed-drift on the beaches. Much rubbish, such as roots of bamboos, however, may be brought down by the rivers; and where the Humboldt Current strikes a bend in the coast we get a repetition, on a smaller scale of the scenes on the Antofagasta beaches. Ancon Bay, for instance, receives much of the floating offal of the south.

The Mangrove Zone (The Coasts of Ecuador and Colombia)

We come now to the mangrove zone which comprises, with the remarkable exception of a long stretch of arid sea-border to the north of the Gulf of Guayaquil, the whole remaining western sea-border of South America, namely, the Ecuadorian and Colombian coasts. My own acquaintance with this region is limited to the estuary of the Guayas or the Guayaquil River and to the southern shore of the Gulf of Guayaquil; but I am able to avail myself of the researches of Baron von Eggers, which cover the entire Ecuadorian coast; and with Ecuador, therefore, I will bring this brief sketch of the littoral flora of one side of a large continent to a conclusion.

The Ecuadorian coast, lying, as Baron von Eggers observes, between the rainless and desert coasts of Peru and the "ewig grüne" coasts of Colombia, may be regarded as a transition-area presenting very varied and complicated conditions. With the cause of the remarkable contrasts exhibited by the strand-flora, not only on the coast of Ecuador, but along the whole west coast of South America through some forty-five degrees of latitude from Patagonia to Colombia, I will presently deal. Here it may be remarked in passing that the Humboldt Current has played the determining part in producing the abnormal climatic conditions to which these remarkable contrasts in the strand-flora of this coast of the continent are mainly due.

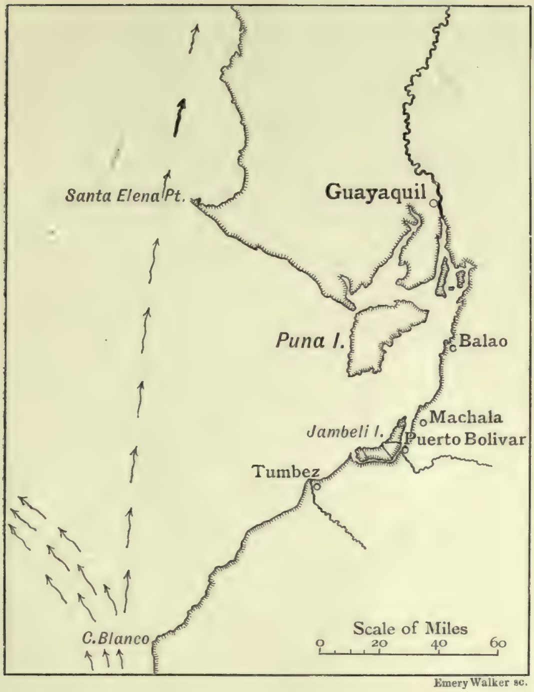
The mangrove zone, marking a more or less abrupt transition from a region of drought and semi-sterility to one of humidity and rank tropical vegetation, begins about lat. 3° 30′ S, that is, in the vicinity of Tumbez, or perhaps nearer the boundary-line between Ecuador and Peru in lat. 3° 20′ (see Note 72). Occupying the southern shore of the Gulf of Guayaquil it extends up the Guayas estuary to Guayaquil and rather beyond. But when we follow the coast of Ecuador northward from the island of Puna towards Santa Elena Point, we come upon one of the most remarkable phenomena presented on the west coast of South America. The dry region begins again and the mangroves disappear; and these conditions continue through about 2½ degrees of latitude until we reach the equator, when the mangrove zone soon recommences, and, as I infer, continues northward without a break to the coast of Central America.

Dealing first with the mangrove districts of the south side of the Gulf of Guayaquil and of the Guayas or Guayaquil estuary, we may observe that probably in few localities of the globe have the forces of nature worked more in unison to produce the conditions favouring the growth of the mangrove. The reason why this particular locality has been thus favoured will be discussed later on in this chapter. I may here obsérve that Baron von Eggers was so struck with the exceptional features of the mangrove-growth in this region that he was inclined to look for the American centre of the genus Rhizophora, the prevailing mangrove, in the estuary of the Guayas River.

I will not enter into a detailed description of the mangrove-formation of this coast, which has indeed been given by the German botanist; but I will merely refer to the leading features such as they presented themselves to me. In the first place, reference will be made to the sea-border of the province of Eloro, where I spent nine or ten days, making Puerto Bolivar, the port of Machala, my headquarters—a locality about thirty miles east of Tumbez. Except in the Guayas estuary I have never seen such a magnificent growth of mangrove.

By following the line of light railway that runs about six kilometres inland from Puerto Bolivar to Machala, the capital of the province, we obtain a good section of the mangrove-belt, which may be thus described. The mangrove-swamp proper extends about three kilometres inland. Whilst the small variety ot Rhizophora mangle (mangle chico) immediately fronts the sea, Laguncularia grows on the islets close to the seaward margin of the swamp. When we enter one of the numerous broad creeks that intersect the border of the mangrove-belt we soon find ourselves in the true mangrove forest, where prevail tall trees of Rhizophora mangle (mangle grande) that rise to a height of 70 or 80 feet or more. Gloomy as the depths of the swamp are, they acquire quite a funereal aspect, the branches of the trees being draped with pendent Tillandsias. These long, hair-like, tangled growths hang vertically from the branches of the trees and may be 20 or 30 feet in length. In the rear of the zone of tall mangroves we come upon a more open district of the swamp. The forest proper gives place to a tract occupied by small trees of Rhizophora, Laguncularia, and Avicennia, with here and there whole acres occupied only by the shrubby Salicornia peruviana which attains the height of a man.

Here terminates the mangrove-swamp proper, and about three



Rough Plan of the Gulf of Guayaquil.

(The main stream of the Humboldt current, as indicated by the arrows, turns off to the north-west at Cape Blanco; whilst a small branch crosses the mouth of the Gulf of Guayaquil and flows along the Ecuador coast north of Santa Elena Point.)

kilometres from the sea it passes gradually into a region of extensive bare mud-flats which are penetrated by salt-water creeks, two or three yards across and a foot or two in depth, that are bordered by low and shrubby Avicennias, the Salicornia bushes above noted, and dwarfed trees of Rhizophora mangle only four or five feet high. These flats, which are evidently only overflowed by the sea at the higher spring tides, were at the time of my visits much sun-cracked and in some parts incrusted with salt; but the mud was rather soft, and in places Sesuvium portulacastrum and Batis maritima flourished in quantity on it. These mud-flats, about two kilometres across, pass by degrees into the low-lying level district known as the Machala plains, on which the capital of the province is built. Here the soil is dryish, and, notwithstanding that it displays on its surface when exposed to the sun a white saline efflorescence, a dry jungle type of vegetation of the xerophilous character here thrives. I noticed casually the Algaroba (Prosopis), a yellow-flowered Cordia, cacti of the Opuntia and Cereus kinds, besides several small trees and shrubs often thorny.

These Machala plains, on account of the fine saline incrustation above mentioned, are of much interest, since at a distance of six kilometres from the coast they thus display on their surface the effect of sea-water infiltration, their level above the sea being only a few feet. We have seen the three stages of this infiltration landward of sea-water: first, the mangrove-swamps daily overflowed by the tide; second, the mud-flats behind them which are only overflowed by the fortnightly spring-tides; third, the vegetated plains behind all, which are sufficiently raised to be above the reach of the tides, but which are nevertheless soaked with sea-water that displays its presence in the salt left by evaporation on the surface of the soil.

But another interesting point is here raised. At the back of the mangrove-belt, in most parts of the world, we usually find a particularly rank and luxuriant vegetation where the Scitamineæ often take a leading part; whereas on the sea-border of this part of Ecuador the mangrove-swamps pass gradually into arid saliniferous plains. With this singular fact is to be associated the circumstance that we see here in operation, some four or five miles from the coast, a process by which great quantities of sea-salts are accumulating below the surface. This may possibly be concerned with the origin of the great saline deposits of Northern Chile. However this may be, there is some reason for believing—and I

understand that this is the opinion of Dr. Wolff, the historio-geographer of Ecuador—that in the course of ages the tendency will be towards an extension of the dry, sterile regions of Northern Peru into Ecuador. This subject is referred to again in a later page of this chapter.

Whilst in this neighbourhood I made the ascent for some fifteen miles of the Santa Rosa River, which opens into the sea near Puerto Bolivar. It is a tidal estuary that has no proportion in size to the small river that enters it. In its lower third we passed at first between long mangrove-islands formed almost entirely, as viewed from the boat, of the tall Rhizophora trees draped with Tillandsias, and presenting really a magnificent spectacle. In the middle third we were penetrating into the rear of the mangrove-belt. The giant swamp-fern (Chrysodium aureum) abounded, and here and there we passed by a patch entirely held by the large shrubs of Salicornia peruviana. The tall Rhizophora trees were replaced by the short variety, the "mangle chico," which ceased altogether about ten miles from the mouth of the estuary, but probably only about five miles from the nearest part of the coast. The water at the place where the Rhizophora trees ceased was evidently quite fresh during nine out of the twelve hours, being only salt in the latter part of the rising tide. Above the mangroves, in the upper third of the ascent, Hibiscus tiliaceus, with Chrysodium aureum, flourished on the banks. The shallows at the margins were occupied by a considerable variety of semi-aquatic and other plants, such as Pontederia (two species); one of the Alismaceæ, with the flower and fruit of Sagittaria and the leaves of Alisma; Typha, Polygonum, and an Amaryllid like Crinum. Plants of Pistia and Pontederia floated in the stream.

I have said enough to give a general idea of the composition of the mangrove-belt of the Ecuador littoral, and will refer but briefly to the mangroves and other river-side plants in the neighbourhood of the city of Guayaquil, some forty miles up the Guayas estuary. As I have remarked in Note 38, the water of the river off the city is usually quite fresh except at high water; but the sea has much freer access to the channels at the back of Guayaquil, where at high water the density was 1·014. In these channels are displayed the typical mangrove formation, trees of Rhizophora mangle bordering the water, whilst behind they are mingled with Avicennia tomentosa and Laguncularia. On the banks of the main river, where they are overflowed at high water, Anona paludosa was the most frequent tree, being associated with the Rhizophora, Hibiscus

tiliaceus, and other trees. Above the city, Polygonum glabrum was growing in dense masses at the river's edge, whilst Pontederia and Pistia flourished on the low muddy banks and floated in quantities in the river.

Before quitting the subject of the mangrove-formation of Ecuador, I will refer shortly to the two varieties of Rhizophora mangle that here occur. Baron von Eggers received the impression that the common type of this species, a low tree bordering the coast, did not exist in Ecuador, such a type as he says is characteristic of the West Indies and of Central America, and, I may add, also of Fiji. The species he regards as acquiring a new facies in Ecuador, where it exists as tall forest-trees, branchless for half their height, and exhibiting other divergent characters. However, I found that the common type of the species occurs normally on the coast in the vicinity of Puerto Bolivar, thirty miles east of Tumbez, a district above described.

There are two distinct forms of Rhizophora mangle exhibited in the mangrove-belt of the coasts around Puerto Bolivar. One of them, which the indigenes name "mangle chico," is a small tree, 10 to 15 feet high, with useless timber, that immediately borders the sea, and, in fact, largely forms the margin of the swamp, not only on its seaward side, but also on the land side, where it passes into drier ground. The other, the "mangle grande," a tall tree reaching to 60 or 80 and sometimes perhaps to 100 feet in height, composes the interior, and indeed the bulk, of the mangrove-belt, and possesses a hard and durable timber much employed in the district.

Distinct as these two types are, it is not difficult to find intermediate forms, and, in truth, in some localities they prevail. But the interesting point is that this peculiar Ecuadorian type of the species, a type that attracted the attention of the eminent German botanist, comes near the "Selala," the mysterious seedless Rhizophora of the Fijian swamps—a subject fully discussed in Chapter XXX., where I have compared the Fijian and Ecuadorian Rhizophoras. Both the "Selala" of Fiji and the "mangle grande" of Ecuador are intermediate between the American Rhizophora mangle and the Asiatic R. mucronata, resembling the last in their inflorescence, but in other points approaching the American species. The "Selala," however, comes nearer to the Asiatic tree, whilst the "mangle grande" comes nearer to the American tree. Unlike the Fijian tree, that of Ecuador is not sterile, but matures its fruit; and it displays no evidence of the vegetative reproduction so characteristic of the "Selala."

Sandy beaches are not common on the mangrove-fronted shores of the south side of the Gulf of Guayaquil. However, on the seaward side of the long low mangrove island of Jambeli, on which the lighthouse is placed off Puerto Bolivar, there is a long stretch of beach of whitish, mainly non-calcareous, sand. The Coco palms behind the beach give the coast quite the aspect of a Pacific island strand. Ipomea pes capræ flourishes on the sand nearest to the sea; and immediately behind, the beach is more or less occupied by a Cyperus 2 to 3 feet high, and by Canavalia obtusifolia. Further back grows a small Acacia tree, and behind it the yellow-flowered Cordia tree of the district; and in the rear of all lie extensive mud-flats, partly occupied by stunted bushes of Avicennia tomentosa and by Sesuvium portulacastrum, which in their turn pass into the mangrove-swamps.

On account of the enormous amount of drift of all descriptions that is carried to the sea by the Guayas or Guayaquil River, floating vegetable materials are abundant in the Gulf of Guayaquil, and are thrown up in quantity on the coasts of Ecuador. One of the most interesting spectacles at Guayaquil is presented by the floating river-drift. Huge tree-trunks and floating islets, the last-named ranging from 3 or 4 to 30 or 40 feet or more across, were, at the time of my visit in February, being carried to and fro unceasingly in front of the city by the tide, gradually making their way down the river, and ultimately reaching the open waters of the gulf. Floating plants of Pistia were in abundance; and their fate when they reached the sea must have been tragical. The islets were exceedingly interesting; they were evidently formed of materials lifted up bodily from the shallows at the margin of the river, and then carried off in the stream. They were mainly composed of two species of Pontederia and of Polygonum glabrum in the position of growth; the first often in flower. Pistia and a variety of smaller plants nestled among them, such as Salvinia, portions of Azolla, Lemna, &c.; and in one islet I noticed, oddly enough, the growing rhizome of a sensitive plant (Mimosa pudica). A great quantity of floating seeds collect amongst the roots and stems of the plants composing the islets, and here I obtained much of the smaller seed-drift.

Most frequent in the floating drift of the river at Guayaquil were the seeds of Anona paludosa, often in a germinating condition. The seeds are liberated by the decay of the floating fruit, which was also common in the drift. Amongst the larger materials were the seeds of Entada scandens and of Mucuna; the empty

seeds of the vegetable-ivory palm (Phytelephas macrocarpa), the sound seed possessing no floating power; the "stones" of Spondias lutea, L., as identified by Mr. Holland, of the Kew Museum; the empty small nuts of several palms, including, apparently, Oreodoxa, &c. Amongst miscellaneous materials were small gourds, which are referred to in Note 47, and an occasional empty cacao fruit. Smaller seeds were also abundant, and included those of Hibiscus tiliaceus, Erythrina, Vigna, Ipomea, and others. Carried into the river from the neighbouring mangrove-creeks, where they abound, there were floating seedlings of Rhizophora and Avicennia, fruits of Laguncularia often germinating, and the seeded joints of Salicornia peruviana.

There was of course, in addition, much that was strange in the floating drift of the Guayas River, which received its contributions not only from the river-side vegetation and the neighbouring mangrove-swamps, but also from the interior mountain ranges culminating in Chimborazo, the slopes of which are drained by its tributaries. I had several opportunities of meeting the drift of the Guayas River in the open waters of the Gulf of Guayaquil. Much of it is carried along the south side of the gulf; and I picked up at sea, ten to twenty miles from the mouth of the estuary, many of the things above enumerated, such as Erythrina and Mucuna seeds, seeds of Hibiscus tiliaceus, the empty vegetable-ivory seeds, the seedlings of Rhizophora and Avicennia, and the germinating fruits of Laguncularia and Salicornia peruviana. Much of these materials mingled with local drift is stranded on the long beach of Jambeli Island, thirty miles from the mouth of the estuary. Here, besides the seeds of Canavalia obtusifolia and Ipomea pes capræ derived from the locality, I found the seedlings of Rhizophora and Avicennia, and the fruits of Laguncularia and Salicornia peruviana, that might have been in part derived from the adjacent swamps, as well as much of the drift of the Guayas River, such as the seeds of Anona paludosa, Entada scandens, Erythrina, and Mucuna, the small gourds, the same small palm-nuts, the empty seeds of Phytelephas, the "stones" of Spondias lutea, and much other material previously familiar to me, but nowhere a sign of the floating Pistias and of the flowering Pontederia islets of that estuary.

The Stretch of Dry Coast from the Vicinity of Puna Island to the Equator.—This remarkable piece of sea-border, covering nearly three degrees of latitude, and in its aridity and general character recalling the sterile sea-coast of Peru, is placed

between the humid mangrove-fronted coast of the Guayas estuary and the similarly humid and mangrove-fronted coasts of Northern Ecuador and Colombia. The mangrove seems to be almost absent from this stretch of dry coast. Mr. F. P. Walker, of the Santa Elena Cable Station, tells me that some time ago a little mangrove-growth existed near the Point, but that it has disappeared; and Baron von Eggers implies the absence of mangroves from the whole coast. The first-named speaks of the dry character of the coast district from Santa Elena Point to within half a degree of the equator; and the last-named, in his description of the coast, mentions cacti and thorny plants as typical of the vegetation. Since this region represents a typical locality where the direct influence of the Humboldt current on the climate of almost the whole west coast of South America can be put to the proof, I will refer to its peculiar climatic conditions below in my discussion of the general question, and will here content myself with saying that on this dry portion of the coast of Ecuador we have reproduced, but in a less pronounced degree, the climatic conditions of the coast of Peru.

The Humboldt or Peruvian Current and the Climate of the West Coast of South America.—The question we will now briefly consider is one that is concerned with the determining causes of the singular distribution of coast-plants on the west coast of South America. The reader will have already seen that the matter is an affair of climate; but it is an affair of climate in which (although it affects forty or more degrees of latitude), latitude, in a general sense, scarcely counts. All the naturalists, from Humboldt onward, who have sojourned in this region of the globe have displayed a deep interest in this subject; and I suppose there can be no region of the globe where there are so many climatic anomalies as interesting to the meteorologist. Here, for instance, might be obtained materials for solving the irritating mystery of a London fog; and if the suggestion of Baron von Eggers, before alluded to, is carried out, and a station is established by the Meteorological Societies of Europe and America at some suitable locality like Santa Elena on the coast of Ecuador, we might obtain, among other results, another line of investigating the causes of the fogs of our metropolis, a subject about which Captain Carpenter has recently made an important preliminary inquiry.

I will assume that my readers are already acquainted with the nature of the problem to be discussed relating to the climate of the west coast of South America, and that they are familiar with the

view generally held that the aridity of this extensive coast region, stretching from the thirtieth parallel of south latitude to the equator, arises from the loss by the trade-winds of all their moisture in the interior of the continent before reaching the western countries of Chile and Peru. Mr. Ball, in his book on South America, opposed this view, though from reasons only partially valid, since he instanced the Ecuador coast as being, contrary to the theory, a wet coast, whereas we know that a large stretch of it is arid and not unlike Peru. The parting of the ways in this discussion lies in the answer to the query, Why should the south-east trade carry so much moisture to the east side of South America, whilst the south-west winds, that are equally prevalent on the west coast of the continent, are drying winds which convert the sea-border into a desert, as in Northern Chile, or into a region of semi-sterility, as in the instance of Peru? Other things being equal, we should expect both sea-borders of the continent in these latitudes to be well watered. In the answer to the question why the south-east trade should be a wet wind and the south-west wind a dry one lies a fatal objection to the prevailing view.

When Professor Davis, in his article on North America in the *Encyclopædia Britannica* (vol. 25), observes in connection with the arid coast regions on the west side of the continent that the southerly flow of the winds along the Pacific coast gives them a drying quality, thus causing the extension to the coast in South California and in North Mexico of the arid regions of the interior, he seems to imply that these winds acquire their drying capacity in flowing from cooler to warmer latitudes. On this view all trade-winds should be drying winds, whereas the reverse would appear to be the case.

There is some condition, present on one coast of the South American continent and absent on the other, which determines why a southerly wind, blowing landward, is in the one case moist and in the other dry. According to my own view the winds of the arid coast regions of western North America cross the cool waters of the Californian current, and thus acquire their drying quality on striking a sea-border more highly heated than the winds themselves. On the tropical west coast of South America the winds also become drying winds by passing over the cold waters of the Peruvian or Humboldt current, where mists are in consequence of frequent occurrence; and on striking the more highly heated land-surface at the sea-border the moving air does not part with any more moisture until an altitude of some thousands of feet above

the sea is reached, when the cloud-belt forms. On the mountains bordering the coast of the Antofagasta province, in January, the clouds gathered at an elevation of 4,000 to 5,000 feet. Perhaps the best way to contrast the east and west coasts of tropical South America in this respect would be to say that whilst the wind blows landward in both regions, the land is the condenser on the east side, and the sea, owing to the interposition of the cold Humboldt current, is the condenser on the west side.

During a fortnight spent in February at Ancon, about twenty miles north of Callao, I noticed that with the prevailing cool south-westerly wind the coast was clear, but it was misty at sea. On the few days when there were warm westerly and north-westerly breezes, the weather was thick at sea; and if this condition was pronounced, the whole coast was enveloped in mist; but more usually the coast-line was fairly clear except at the promontories, along the sides of which clouds blown in from the sea rolled in lines inland, not generally attaining an elevation over 300 or 400 feet, but sometimes reaching 900 or 1,000 feet, and gradually disappearing a mile or two inside the coast-line. These sea-born clouds thus vanished as they traversed the more highly heated land-surface; and the air-current continuing its inland course mounted the slopes of the adjacent mountain ranges of the Andes, some three or four miles from the coast, until at an altitude of some 5,000 or 6,000 feet condensation again occurred and the cloud-belt was formed at those cooler levels.

From the summit of a range rising to a height of about 2,500 feet to the north-west of Lima I had presented to me a splendid spectacle, on February 12th, in the formation of the coast-belt of clouds. The forenoon was clear, but about 2 p.m. the sea-born clouds began to roll inland, concealing the lower two-thirds of the island of San Lorenzo, which has an elevation of almost 1,400 feet, and completely covering up Callao and the low country bordering the sea, but extending only a mile or two from the coast-line. The dense cloud that covered Callao appeared, as I looked down upon it from my mountain-peak, like a billowy field of snow sparkling in the sun, with the summit of San Lorenzo standing out like some bare alpine summit from amidst the snows. Yet beneath that dazzling covering Callao lay all in gloom; whilst only six miles up the broad valley of the Rimac the city of Lima stood in a blaze of sunlight, its domes and towers reflecting back the light as I looked at the strange contrast it presented with the buried city of the coast. The mystery of a London fog seemed to

lie unfolded at my feet, ready for the man who can read the signs aright.

That the mere presence of a cold current on a coast with the winds blowing off the land (as in the case of the Labrador current, which extends down the Atlantic coast of North America to Cape Hatteras and beyond) produces no sterilising effect on the vegetation of the sea-border of a continent is well brought out in the beautifully executed maps in Prof. Russell's recent work on North America. The essential condition for producing sterility on the sea-border of a continent is not only that the waters of a cold current should wash its coasts, but that the regular winds should blow landward across its cool surface. These are what we find on the west coast of South America.

Not with the hope of adding anything new to our knowledge of the climatology of this region, but with the purpose of becoming personally acquainted with the problem involved, I paid considerable attention to this subject during the three months passed on the west coast of South America between Port Valdivia and Guayaquil. It was not until I had dropped my thermometer into the cool water of the Humboldt current and had watched the formation of the fogs on the sterile coast of Peru that the real nature of the problem presented itself. From the pages of a work like Tschudi's *Travels in Peru* one acquires an excellent idea of the extraordinary climatic conditions of this region, and the same may be said of the narratives of Darwin and other travellers; but it is necessary to be brought into personal contact with these conditions before one can appreciate their significance.

As is well known, says Baron von Eggers, the Humboldt current explains the anomalous climate of the coast of Peru, and one may add of North Chile and Ecuador. The current, which represents the extension northwards of the west wind-drift of the Roaring Forties (see Dickson in *Encycl. Brit.*, xxxi. 404; and Admiralty Current Charts of the Pacific), begins on the coast between the 33rd and 40th parallels of south latitude, according to the season. North of Valdivia, as we approach Valparaiso, in lat. 33° S., the effect of its presence is at once seen in the increasing dryness of the climate and in the alteration in the character of the vegetation. It has, however, been shown that the current needs the co-operation of the prevailing southerly and westerly winds as they blow landward over its cool waters. On the coast of Peru these moist winds often generate fog and mist as they cross the current. They reach the coast as drying winds, having a tempera-

ture much cooler than the lower coast regions; and the air-currents do not precipitate any moisture on the land until an elevation of 4,000 to 6,000 feet is attained where the cloud-belt is formed.

In order to establish this theory it is, however, necessary to show that when the Humboldt current leaves the coast normal conditions of humidity occur, to which the vegetation responds, and that when the current strikes the coast again the conditions of aridity reappear. In its course northward the current divides off Cape Blanco, the principal mass of its waters making towards the Galapagos Group, whilst the remainder, after crossing the Gulf of Guayaquil, flow along the coast of Ecuador between Santa Elena and the equator. Now, it is along this stretch of the Ecuador coast that the conditions of aridity reappear and that the climate of the Peruvian sea-border is in a modified form reproduced. In the interior of the Gulf of Guayaquil, on the other hand, where the sea-border is no longer subjected to the influence of the cold waters of the Humboldt current, the genius of the tropics, repressed through so many degrees of latitude, bursts its bonds, and presents us with a spectacle of littoral vegetation that, so far as mangrove-growth is concerned, is probably unrivalled on our globe.

This contrast is well shown in the mean annual temperatures on the opposite sides of the Gulf of Guayaquil. Baron von Eggers, quoting Dr. Wolff, states that whilst the mean for the year at Puna is about 75° F., and at Santa Elena about 73°, on the south side of the gulf at Balao it is several degrees warmer and is evidently not under 80°. The mean temperature for the second week of March during my sojourn at Puerto Bolivar, which is near the beginning of the mangrove region on the south side of the gulf, was 79°, the mean daily range being 74° to 83·5°. This stretch of dry coast reaching north from Puna to the equatoı is evidently regarded by Baron von Eggers and others who have studied the climatology of Ecuador as the critical area required to confirm the theory connecting the aridity of the west coast of South America with the Humboldt current. Here the sea for the greater part of the year has a temperature (according to the British Admiralty chart of surface-temperatures) of 70° to 75°; the mean temperature of the air is 73° to 75°; the rainy season, instead of covering a period of six months and over, as in the humid regions north and south of this coast, has a duration of only two or three months; the prevailing wind is south-west; whilst the direct influence of the cool waters of the current is shown in the general cloudiness that

prevails during the last half of the year and in the drizzling mists that are frequent from June to October. Reference has already been made to the manner in which the vegetation on this dry coast of Ecuador responds to the arid conditions, as, for instance, in the absence of mangroves and in the prevailing character of the plants of the sea-border, cacti, thorny plants, and such like. For my information on this exceedingly interesting tract of coast, which is the test-ground of the Humboldt current theory, I am indebted to the papers of Baron von Eggers (see end of this volume) and to Mr. F. P. Walker, of the Central and South American Telegraph Company's Station at Santa Elena, who very kindly communicated with me by letter. Some additional remarks are given in Note 73, and my own observations on the temperature of the Humboldt current from Antofagasta northward are summarised in Note 74.

Before quitting the Ecuador coast a word may be said relating to the prediction of Villavicencio that the climate of this sea-border will assimilate itself to that of the rainless coasts of Peru. This is, I believe, also the opinion expressed by Dr. Wolff in his *Geografia y Geologia del Ecuador* (Leipzig, 1892); and it is referred to by Mr. Webster in his article on Ecuador in the seventh volume of the *Encyclopædia Britannica.* There is a prevailing impression amongst the more observing residents that I met in the Ecuadorian province of Eloro, on the Peruvian border, that the country is drying up. A few pages back I have described how in the Machala district of this province the mangrove-belt passes landward into an arid region suggestive of the sea-border of Peru. This transition is startling to one who expects to find behind the mangrove-belt, as he would find in most parts of the world, a humid region where Nature revels in the rank luxuriance of plant-growth. This is, however, not always the case, since on the lee or dry sides of the large islands of Fiji the mangrove-belt is backed by extensive arid plains, for an explanation of which, as I have shown in Note 22, we have to appeal rather to the hygrometer than to the rain-gauge. This is true also of Ecuador; but whilst the reason is intelligible enough in Fiji, it only carries us a step farther back in the case of the Machala plains in Ecuador. These plains are continuous with similar districts across the Peruvian border where they reach the coast; and if the reader will refer again to my description of the section of the mangrove-belt and the plains in its rear from Puerto Bolivar to Machala, he will incline to the view that the desiccation of the sea-border of Ecuador is now in progress.

Evidence of a more direct nature could doubtless be supplied by those who have long resided on the coast of Ecuador, and in illustration I will give an extract from one of Mr. Walker's letters dated May, 1904, from Santa Elena.—"The rainfall here might for the last ten years be put down at two showers per year. It is said that the last good rainy season was in 1891. The inhabitants say that formerly it always rained enough to make the grass grow every year, but during the eleven years I have been here there appears to be a marked falling off of the rainfall."

It has been only possible to touch the fringe of this interesting question here; but from the standpoint of the study of the littoral flora of the west coast of South America it is of some importance. Immediately behind the epoch of the present marine molluscan fauna of this coast there lies an age when, as we learn from Philippi, the shells of Chile were more akin to those of the Atlantic and Mediterranean faunas than to those now found on the Chilian coasts. The transition is a sudden one; and amongst other explanations of this strange transformation Suess suggests the sealing up of a communication through the Panama isthmus by volcanic eruptions and the appearance of the Humboldt current (*Das Antlitz der Erde*, French edit. by Margerie, ii. 825). May it not be, my readers may ask, that the west coast of South America is still in the age of progressive sterility; and that before this age began Peru possessed a normal tropical strand-flora? It has been remarked in Chapter VIII. that the same species of mangroves occur on both the Atlantic and Pacific coasts of America, and that at all events their present distribution belongs to an age when the Gulf of Mexico was in communication with the Pacific Ocean. May we not, again, suppose that in that age the mangroves extended far south on the coast of Peru, just as they do now on the coast of Brazil?

Coral reefs are stated not to exist in tropical latitudes on the west coast of South America in our own day; but we might almost expect that at the close of the Tertiary period, and perhaps before the appearance of the Humboldt current, they existed with the mangroves on the coast of Peru. As bearing on the subject of a change of climate on that coast in times geologically not remote, I may allude to the circumstance, which is discussed more in detail in Note 75, that I found, sometimes in fair quantity, blocks of massive coral, long since dead, much pierced by boring shells, and in places undergoing a chemical change, at Arica (lat. 18° 25′ S.), at Callao (12° 3′ S.), and at Ancon (11° 45′ S.) on the coast of Peru.

These masses, which varied from a few inches to two or three feet in size, gave me the impression of having been torn off the bottom, in some cases in recent times, in others perhaps centuries ago, by the huge sea-waves that from time to time overwhelm this coast. At Ancon, where they were sufficiently abundant to be used for bordering the flower beds in the hotel garden, they were most numerous in the vicinity of a rocky spur of andesite that protruded from the beach between the tide levels and was more or less covered at high water. A few paces inland from the beach some of these coral masses, evidently stranded long ago, were undergoing that queer process of disintegration which everything calcareous seems to undergo on the beaches and plains of this almost rainless coast. Like the bones of the Incas lying bleaching on the neighbouring plains, like the sea-shells and bones of bird and beast cast up long ago on the beach, they were falling to powder where they lay, and the coral fragment lay often in the midst of its own *débris*. The blocks on the beach proper were for the most part still hard and compact, and the same may be said of those observed on the beaches of Callao and Arica.

The corals were quite different from those with which I was familiar in the reefs of the Pacific islands, and, bearing in mind the known distribution of coral reefs, I was a little dubious about them. Accordingly I sent some specimens to the British Museum, and Mr. Jeffrey Bell has kindly informed me that they seem to be decayed and much injured perforated examples of Porites. When powdered they effervesce in an acid, but the bulk of the material remains undissolved.

No more eloquent testimony could be afforded of the rainless climate than these corals crumbling on the Ancon plains when washed a few paces inland from the beach. They could be noticed in all stages of disintegration from the block surrounded by a little line of disintegrated material, representing the initial products of its own decay, to the crumbling mass, almost friable in the fingers, that was lying in the midst of its own dust and loose polyp-tubes, and finally to the little mound of *débris* that alone remained. Mr. Darwin, in his *Journal of Researches* (chap. xvi.), refers to a similar process of decay in the elevated shell-beds of San Lorenzo, off the coast of Callao. On the higher terraces a layer of saline powder, consisting of sulphates and muriates of lime and soda but with very little carbonate of lime, was the sole indication of the shell-beds. Dry climatic conditions at the sea-

border evidently favour, as he observes, the early decay of exposed calcareous remains.

The Shore-plants and Stranded Seed-drift of the Panama Isthmus.

I spent two days at Panama and two days at Colon in examining the neighbouring beaches and estuaries of the Pacific and Atlantic coasts of the isthmus. On the Panama side the mangrove-belt was formed on the seaward border of "mangle chico" (the small prevailing type of Rhizophora mangle), Laguncularia, and Avicennia; whilst behind it passed into extensive swampy tracts occupied by the Swamp Fern (Chrysodium aureum), Hibiscus tiliaceus, and other plants. On the Colon or Atlantic side the mangrove-belt had precisely the same composition and presented the same species, Rhizophora and Avicennia usually forming the outposts on the reef-flat, whilst Laguncularia was abundant in the rear. In the estuary of the Rio Chagres, Rhizophora and Laguncularia were abundant near the mouth, and Chrysodium aureum and Hibiscus tiliaceus by the waterside higher up. Dr. Seemann, in his volume on the botany of the voyage of H.M.S. *Herald*, observes that the species of Laguncularia common on both the Atlantic and Pacific coasts of the Panama isthmus is L. racemosa. This species differs in the form of its fruit from the Ecuador tree. Laguncularia racemosa, Rhizophora mangle, and I may add Anona paludosa and Conocarpus erecta, are all plants of the mangrove-formation that occur not only on the Pacific and Atlantic coasts of America but also on the west coast of Africa. It is likely, I may add, that the "mangle grande," the Ecuadorian type of Rhizophora mangle, exists in the Panama isthmus, since in the higher part of the estuary of the Chagres I found trees approaching it in characters.

Amongst the plants growing on the Panama beaches I noticed Canavalia obtusifolia, Hibiscus tiliaceus, and Ipomea pes capræ, all of which occur also on the Atlantic side of the isthmus. The Manchineel (Hippomanes mancinella), found also on the Atlantic side of the continent, grows on the Panama beaches. Its fruits, which look like crab-apples, lose their outer fleshy covering when drying on the sand. Not being familiar with this poisonous tree, I allowed some of the milky sap of the fruits to touch the skin, and suffered great pain for five or six hours. The fruit possesses an inner coat of air-bearing cork-like tissue; and the stone, if I may so term it, thus acquires great floating power. I kept some

afloat in sea-water for five weeks, and no doubt they will float for months.

The seed-drift to be observed stranded on the beaches and floating in the estuaries on both sides of the isthmus is, generally speaking, the same—a circumstance of great importance in plant-distribution, since we can here see rivers bringing down the same seeds from the same "divide" to the shores of the Pacific and Atlantic oceans. In the case of a plant like Entada scandens, which grows in the interior, this is a matter of much interest, as it thus possesses here a centre of dispersal from which its seeds can be carried by the currents eastward to the West African coast and westward across the Pacific to Malaya and (given time) around the shores of the Indian Ocean to the East African coast. In describing the possible routes of dispersion from this centre I have described the distribution of the species.

I am indebted to Mr. Holland, of the Kew Museum, for the identification of some of the drift-seeds and fruits collected by me on the isthmus, those identified by him being followed by the letter H. On the beaches and floating in the estuaries on both sides of the isthmus I found Rhizophora seedlings; seeds of Entada scandens and Mucuna urens (medic.), H.; seedvessels of Spondias lutea (Linn.), H.; Prioria copaifera (Griseb.), H., with decayed seed; and the empty nuts, 1½ to 2 inches in size, of more than one species of Astrocaryum, H. Although in the case of the two last-named genera the seedvessels were useless for dispersal, being evidently brought down from the interior by the rivers, they serve to illustrate the important principle that the rivers bring down the same seed-drift on both the Atlantic and Pacific coasts of Central America. Mr. Hemsley includes amongst the seed-drift stranded on the coast of Jamaica the seedvessels of Spondias (probably S. lutea) and of Astrocaryum (*Bot. Chall. Exped.*, iv. 299, 304).

Those of Spondias lutea were found by me floating in the Guayaquil River and stranded on the beaches of Ecuador and of the Pacific and Atlantic coasts of the Panama isthmus. This is the Hog-plum, which in tropical America and the West Indies is both wild and cultivated. Its buoyant "stone" has a covering of cork-like air-bearing tissue. This is a remarkable case of non-adaptation in the matter of buoyancy. The seedvessels cut across contained sound seeds; and they are provided with the essential qualities of "long floaters."

Summary.

(1) The strand-district of the west coast of South America is divided into four zones:—

(*a*) The Convolvulus soldanella zone of Southern Chile.

(*b*) The Desert or Plantless zone of Northern Chile.

(*c*) The Sesuvium zone of Peru.

(*d*) The Mangrove zone of Ecuador and Colombia.

(2) The mangroves do not extend south of Ecuador or, more strictly, south of Tumbez (3° 30′ S.).

(3) The absence of mangroves on the tropical coasts of Chile and Peru is attributed to the Humboldt current, which has so influenced the climate that it has converted the sea-border of North Chile into a desert and that of Peru into a region of semi-sterility.

(4) It is considered that this has been effected through the prevailing winds acquiring drying qualities on crossing the cold waters of the current in tropical latitudes.

(5) To establish this it is shown that when the Humboldt current leaves the coast at Cape Blanco mangroves thrive in the Gulf of Guayaquil, and that when it strikes the coast again near Santa Elena Point and courses along that seaboard to the equator we find the Peruvian conditions of semi-sterility reproduced.

(6) The probability that the arid climate of Peru is in our own time extending northward into Ecuador is pointed out; and from the presence of old coral blocks on the Peruvian beaches it is considered likely that when these corals throve the mangroves extended far down the coast of Peru.

(7) It is shown from the presence of the same species of mangroves on the Pacific and Atlantic coasts of America that there must have been, not long ago, a communication between these two oceans across Central America; but it is at the same time observed that this could not be inferred from shore-plants with buoyant seeds that, like Entada scandens, occur inland, since, although they occur on both sides of the continent, their distribution can be explained by the transport of their seeds by rivers to the Atlantic and Pacific coasts, such as we see in operation on the Panama isthmus in our own day.

(8) Stress is laid on the great development of mangroves in the Gulf of Guayaquil and in the Guayas estuary; and it is

pointed out that there are in this locality two varieties of Rhizophora mangle, a large and a small variety, the first approaching in some of its characters the Asiatic species, R. mucronata, and being akin also to the seedless intermediate form of Fiji.

(9) Amongst other matters dealt with in this chapter are the floating seed-drift of the Guayas or Guayaquil River and the shore plants and stranded seed-drift of the Panama isthmus. From the locality last named we learn that rivers bring down from the interior to the Atlantic and Pacific coasts much the same seed-drift, and that from this centre littoral plants with buoyant seeds can be distributed over the whole tropical zone.

CHAPTER XXXIII

SEED-DISPERSAL AND GEOLOGICAL TIME

The shifting of the source of the Polynesian plants from the New to the Old World.—The floral history of Polynesia stated in terms of geological time.—The suspension of the agencies of dispersal in later periods.—Parallel differentiation in the course of ages of climate, bird, and plant.—New Zealand.—Insects and bats as agents in plant-dispersal.—The effective agency of sea-birds in other regions.—The observations of Ekstam.—The Spitzbergen controversy.—The efficacy of ducks as distributors of aquatic plants.—Summary.

In the matter of the dispersal of seeds by birds in the tropical Pacific, there are at least two questions which my readers must have frequently put to themselves. The one would be concerned with the shifting of the source of the Polynesian plants from America to the Old World, which occurred probably near the close of the Tertiary period. The other would be connected with the suspension of the work of dispersal over a large portion of Polynesia, which has become more and more pronounced as we approach our own day.

Suggested Cause of the Shifting of the Source of the Polynesian Plants from the New to the Old World.—In previous chapters we have discussed the various epochs in the plant-stocking of these islands. There was first the age of Coniferæ, in which the islands of the Western Pacific were only concerned, an age prior to the appearance of the volcanic groups of the Tahitian and Hawaiian regions, and placed in the Secondary period. Then followed, in the Tertiary period, after the birth of Hawaii and Tahiti, and when the island-groups of the Western Pacific were mainly submerged, the general dispersion from America of the Compositæ, Lobeliaceæ, and other orders, now represented only by genera peculiar to the Hawaiian and Tahitian islands. Last of all, towards the close of the Tertiary period, when the island-groups

of the Western Pacific had re-emerged, a general dispersion of Old World plants, mainly Malayan, took place over all the present archipelagoes of the tropical Pacific.

Since the climate of Hawaii must have, to a great extent, shared in the vicissitudes of the continental climates of the northern hemisphere before, during, and after the Glacial epoch, it is assumed that in the Ice Age no tropical plants reached the group, and that only the plants now represented in its mountain-flora could have then reached there. The area of active dispersion of tropical plants was pushed far south. During the Ice period, Indo-Malayan plants doubtless crowded into the equatorial region of the Western Pacific; but, cramped and confined within this limited area, they were cut off by a climatic barrier from the cool latitudes of Hawaii. As the cold ages passed away, migratory birds, confined during that period to the southern hemisphere, would extend their ranges north, sometimes reaching Hawaii, and transporting to it the seeds of New Zealand and Antarctic genera, now represented by endemic species on its mountain-slopes. The Indo-Malayan plants, with the increasing warmth in the climate of the northern hemisphere, would overrun the Pacific, set free from their prison in the south-west portion of that ocean. Dispersal, we might imagine, would be at first very active over the whole ocean.

My point is, then, that whilst the Malayan era of the plant-stocking began after the Ice Age in the northern hemisphere, the dispersion of the New Zealand and Antarctic genera over the Pacific took place during that period; whilst, as before noticed, the dispersion of the Compositæ, Lobeliaceæ, and other orders, represented now in Hawaii by endemic genera, would be pre-Glacial and well back in the Tertiary epoch. I would, therefore, suggest the following scheme, in illustration of the floral history of the tropical Pacific.

(1) The Age of Conifers of the Western Pacific during the Mesozoic period, and before the appearance of the Hawaiian and Tahitian archipelagoes.

(2) The Age of Compositæ and Lobeliaceæ, and of other genera. This is an era of American plants, and it is referred to the Tertiary period. In it only the newly-formed Hawaiian and Tahitian groups shared, the islands of the Western Pacific being largely submerged.

(3) The Age of Malayan plants, regarded as mainly post-Glacial, and subsequent, therefore, to the re-emergence of the Western Pacific islands at the close of the Tertiary period.

Dispersion then was general over the Pacific. The distribution of the New Zealand and Antarctic genera, plants that take a subordinate part in the floras of the Pacific islands, is regarded as having occurred during the glaciation of the northern hemisphere.

On the Suspension of the Agencies of Dispersal in the Tropical Pacific.—If the remark of Drake del Castillo that genera possessing only non-endemic species in the Pacific islands owe their presence in this region to existing agencies of dispersal looks something like a truism, we must remember that, assuming Nature to be uniform in her methods, it involves not merely the original co-operation of the same agencies with genera that own only peculiar species, but also the subsequent suspension of the work of these agencies.

The nature of the connection between freedom of dispersal and specific differentiation is well brought out by Beccari in contrasting the species of Ficus and the palms of Borneo; whilst out of fifty-five species of Ficus collected by him in that island, 30 per cent. were apparently peculiar, 85 per cent. of the 130 Borneo palms had not been found elsewhere. In the English edition of his *Nelle Foreste di Borneo* he says that "the explanation lies in the fact of the facile dissemination of the various species of Ficus through the agency of birds, an explanation which applies to all trees which produce edible fruits specially relished by animals." He shows, also, that the same principle applies within the limits of the genus Ficus, since of those Bornean species known to him as belonging to the section Urostigma, which possesses fruits most preferred by birds (pigeons, hornbills, &c.), nearly all (fourteen out of sixteen) are found elsewhere; whilst of ten species belonging to the section Covellia, where the fruits are more or less hidden and inconspicuous, and with difficulty discovered by birds that would effectively distribute the species, four, at the most, are found elsewhere. "Such facts," he goes on to say, "show that in tropical countries the various kinds of Ficus are, to a large extent, biologically connected with birds, which, perhaps, on their part, also owe some of their peculiarities in the shape of the bill or in the plumage to the nature and coloration of the fruits which form their food."

Whilst Dr. Beccari as a botanist lays especial stress on the biological connection in Malaya between the plant, as illustrated by the genus Ficus, and the bird, Mr. Perkins, as a zoologist, is similarly emphatic on the biological connection in Hawaii between the bird, as illustrated by the peculiar family of the Drepanididæ, and the plant. The plants here are the arborescent Lobeliaceæ and the Freycinetias. To the flowers of the arborescent Lobeliaceæ

the nectar-feeding Drepanids are particularly partial; and the development of the extreme forms of these birds, as Mr. Perkins observes in the *Fauna Hawaiiensis*, "is not comprehensible without a knowledge of the island flora." Not only does he point to the modifications in the form of the bill of the bird in connection with the tubular form of the flowers; but in at least one species of these arborescent Lobeliaceæ he shows that it is dependent on the Drepanid for its fertilisation, and he inclines to the view that changes such as that of lengthening of the bill may have taken place side by side with the increasing length of the tubular flowers. In connection with the Freycinetias of Hawaii, Mr. Perkins regards the bill of the Ou, a finch-like Drepanid of the genus Psittacirostra, as "entirely formed and adapted for the purpose of picking out the component parts" of the fruiting inflorescence.

That in an isolated island-group birds and plants often "differentiate" together is a fact well known in distribution. In Hawaii, for instance, as I learn from Mr. Perkins, quite 45 per cent. of the birds are peculiar; whilst according to Dr. Hillebrand 80 per cent. of the flowering plants are confined to the group. Then, again, in the Galapagos Islands, half of the plants and two-thirds of the birds are confined to that archipelago. At the other end of the series we have the Azores, with about a tenth of its plants peculiar, and about 4 per cent. of its birds peculiar to the islands, and Iceland with no endemic plants and, as far as I can gather, few peculiar birds.

Accepting Mr. Charles Dixon's view (*The Migration of Birds*, 1897) that specific differentiation does not occur along lines of migration, we must assume that the differentiation of the avifauna of an isolated group like Hawaii began with the breaking off of its regular communication through birds with the outside world. I do not consider that in the past these Pacific archipelagoes received their birds in any haphazard fashion, as, for instance, in the guise of stragglers that had lost their way. From the circumstance pointed out to me by Mr. Perkins that 25 of the 67 genera of Hawaiian birds are peculiar, we must postulate a high antiquity for the bird fauna dating far back into the Tertiary period. Mr. Perkins, who kindly supplied me with his general views of the nature of the Hawaiian fauna, tells me that it is "positively oceanic-insular and could be continental only on the supposition that everything continental had been at some time destroyed and that the group had been subsequently re-stocked as would any oceanic island."

The view naturally presents itself that in past ages birds in the Pacific were much more uniform in their characters, and the agencies of dispersal far more active in their operations and far more general in their range than in more recent times, "It may be accepted (says Mr. Dixon) as an axiom of geographical distribution that all existing species are surviving relics of more ancient forms or ancestral types, whose dispersal in a remoter past was more continuous, and whose affinities and characteristics were therefore more homogeneous." I assume that in past ages the differentiation of birds has largely been favoured by differentiation of climate acting through the limitation of their ranges. To these changes, plants, so often biologically connected with birds, have largely responded.

There is, of course, no difficulty in imputing to birds the capacity of reaching Hawaii in the mid-Pacific, and there are many regular migrants now (sea-birds, waders, ducks, &c.). The only difficulty is in the estimation of the time occupied in the trans-oceanic journey. According to Gätke the journey, which is 1,500 to 2,000 miles, ought to be accomplished within the limit of fifteen hours, which he regards as "the longest spell during which a bird is able to remain on the wing without taking sustenance of any kind." As he considers that a bird might cover the 1,600 miles between Newfoundland and Ireland in nine hours (*Heligoland as an Ornithological Observatory*, p. 140), the Hawaiian traverse would offer to him no difficulties. It has frequently occurred to me in this connection that in ancient times, when the volcanoes of the mid-Pacific were in full activity, their light at night-time would have often given a direction to the migrating bird, and that they might have sometimes determined the line of migration across the Pacific.

It has not been possible to discuss here the capacity of pigeons to cross an ocean, a subject bearing directly on the floras of all the Pacific groups (excepting Hawaii, which possesses no indigenous Columbæ) and as concerning these islands generally presenting no difficulty. Dr. H. de Varigny, who amongst his other studies has long displayed an active interest in plant-dispersal, has directed my attention to two very important papers on the flight of pigeons in the *Revue Scientifique*, one by M. A. Thauziès (April 30, 1898) and the other by M. M. Dusolier (Nov. 28, 1903). That land birds, as well as swimmers and waders, cross the Atlantic is well known, and in this connection the reader might profitably consult Prof. Heilprin's *Geographical Distribution of Animals* (vol. 58, *Internat. Sci. Ser.* 1887).

Much might be said of these matters, but it would be out of place here; and I will content myself with stating the view above indicated that the suspension of the agencies of seed-dispersal over the Pacific is probably connected with a general principle affecting the whole plant-world. The tendency in the course of ages has been towards the differentiation of climate, bird, and plant, the range of the bird being largely controlled by the climate, and the range of the plant being mainly dependent on the range of the bird.

It is evident that in some cases the plants themselves may make the endemism of a flora more pronounced by creating their own difficulties and by standing in the way of their own dispersal to outside regions. It has been shown that some of the endemic Hawaiian genera (see Note 68) have deteriorated in their capacity for dispersal by birds; and similar remarks are made with reference to the genera Sicyos (page 365) and Eugenia (page 350). Genera with stone fruits like Elæocarpus possess in the different species stones of various sizes, some of them suitable in point of size for conveyance in a bird's body over an ocean, others so large that one could only predicate for them a limited capacity for distribution by birds over a few hundred miles of sea. One, for instance, could safely assume that species of Elæocarpus, with stones an inch and over in size, that occur in Fiji and Hawaii, are not suited for distribution over an ocean now; whilst other species found in New Zealand and Rarotonga have stones less than half this size, which are quite fitted for distribution by birds over broad tracts of ocean (page 337).

This brings us to discuss the relative difficulties presented from the dispersal-standpoint by the forest floras of Hawaii, Fiji, and New Zealand. It is with the forest floras that nearly all the difficulties of distribution lie; and I hope I shall not be considered presumptuous, or at all events too heterodox, in expressing the opinion that judging from the details given in Kirk's *Forest Flora of New Zealand* those islands present no greater difficulties for the student of plant-distribution, if we exclude the Coniferæ, than either Fiji or Hawaii. Indeed, even with the Conifers included, New Zealand presents fewer problems than Fiji, and Hawaii has its own special difficulties connected with the inland species of the Leguminosæ. There is, on the other hand, no special New Zealand difficulty. It possesses the Conifers in common with Fiji; and it shares with Fiji and Hawaii genera like Elæocarpus and Sideroxylon, that take a foremost place amongst the trees of the Pacific

forest flora presenting puzzling points to the student of distribution. The existence of Elæocarpus in New Zealand admits of a simpler explanation than the occurrence of the same genus in Hawaii. Pandanus in Fiji is a more difficult genus from the standpoint of dispersal than Corynocarpus in New Zealand, and in fact, than any of the non-coniferous genera of forest trees in that region.

Whilst it is likely that birds of the genus Porphyrio have, up to almost recent times, been active in distributing the seeds of New Zealand plants outside the region (see p. 296), it would seem that the fruit-pigeons, as represented by a solitary peculiar species of Carpophaga, have long since ceased to be active in this direction. It is true that Sir W. Buller gives a long list of trees, including Corynocarpus, Elæocarpus, Litsea, Olea, Podocarpus, and many others, the fruits of which are appreciated by this pigeon; but since the bird is confined to this region its efforts in plant-dispersal possess only a local interest. Mr. G. M. Thomson, indeed, has expressed the opinion (*Trans. and Proc. N.Z. Instit.* vol. 33) that in recent times not a single plant has been added through the agency of birds to the New Zealand flora. Besides the regular migratory birds two cuckoos only reach the region, the one from Australia and the other from Polynesia; whilst Australian birds which had managed to survive the long flight across the ocean have been met with only at times on the west coast of the North Island. From the standpoint adopted in this work we should have expected that, with the exception of current-dispersed plants, New Zealand would be out of touch with the world outside. Varied only by occasional inrushes of plants, its history, dating back to the Mesozoic age, has been one of insular isolation.

When, however, we apply the principles of plant-dispersal in the Pacific, deducible from the study of the Hawaiian flora, we learn that the stocking of New Zealand with its plants could have been carried out (with the exception of the Coniferæ and a few other genera like Fagus that are in a geological sense ancient denizens in this region) by the agencies that stocked Hawaii with its flora. New Zealand genera like Elæocarpus, Sideroxylon, Sophora, etc., that are represented in the forests of Hawaii, could not be taken to illustrate any former continental connection. If we, so-to-speak, put the New Zealand forest flora in the Hawaiian sieve, all will pass through with the exception of Fagus, the genera of the Coniferæ, and plants of similar history in high southern latitudes. This residuum belongs more to the palæobotanist than to the student of means of dispersal.

I should be inclined to think that the tropical genera of the New Zealand flora, more especially of the forest flora, reached that region during the glaciation of the northern hemisphere, when the Indo-Malayan plants were, so-to-speak, cornered in the Western Pacific. Yet it must be noted that these are, as a rule, genera that either display an indifference to the varying thermal conditions of different latitudes or are known to at times extend their range beyond the tropics. Thus Elæocarpus and Freycinetia are equally at home in the temperate rain-forests of New Zealand and in the tropical rain-forests of Polynesia and Malaya; whilst widely-spread tropical genera like Pittosporum and Peperomia, that occur in New Zealand, exhibit their power of adaptation to varying climates by extending outside the tropics in other regions and by their vertical range in the Hawaiian mountains, where they are found alike at low elevations a few hundred feet above the sea and at altitudes of 6,000 or 7,000 feet.

All these plants, however, are in a relative sense recent intruders. When the student of dispersal looks at the long list of the conifers of the New Zealand forest flora and reflects that he knows but little of their means of dispersal, and that if his acquaintance were far greater it would not avail him much, he has no choice but to take his place behind the earlier investigators of the flora, and to see in these trees evidence in favour of a remote continental period, probably referable to the mesozoic age.

A Discussion of some Means of Dispersal.—Not many authors seem to have discussed the possibility of insects as agents of seed-dispersal in the Pacific. They appear to me quite suited for transporting the spores of ferns and lycopods as well as the minute seeds of plants like the orchids and the begonias. Darwin, who allowed few possible means of dispersal to escape his notice, procured the germination, as my readers will remember, of grass seeds found in the dung of Natal locusts. When on the barren summit of Mauna Loa, I noticed that the recently dead bodies of some butterflies, that had been carried up the slopes from the forests below by the "southerly updraught," were already attacked by bugs, parasites that must have been transported from the lower regions by some of the numerous larger insects that are blown up the slopes.

In Note 61 the occurrence of the wind-blown insects on the summit of Mauna Loa is described. That insects can be transported into the upper regions of the atmosphere by ascending air-currents was long ago remarked by Humboldt, and the subject

has been discussed with his usual acumen by Whymper (*Travels amongst the Great Andes of the Equator*). Carried along in the higher air-currents these insects might finally be deposited at places far distant from their home. One reads occasionally extraordinary accounts of a rain of insects. A very circumstantial account was given to me when I was on Keeling Atoll of a shower of dragon-flies that fell on the islands, their remains being found in quantities in the lagoon. Dragon-flies, it is known, are often found at sea far from land, and one species has been observed nearly all over the world, including the Pacific islands. In this connection it is interesting to recall Mr. M'Lachlan's remark in his article on the dragon-fly in the seventh volume of the *Encyclopædia Britannica* that some of the earliest fossil forms seem to have been washed ashore after having been drowned at sea.

Another creature that has been often ignored as a possible agent in seed-dispersal is the bat. Bats are found all over the world, including the oceanic groups, and one can scarcely doubt that they must have often transported seeds, at all events in their hair. They are found at times high up in mountainous regions, and Sir H. Johnston, in his recent work on the Uganda Protectorate, refers to the occurrence of bats at an altitude of 13,000 feet. The large frugivorous bats (Pteropidæ) are known to be very destructive feeders ; but I doubt whether they swallow the seeds. Dr. Warburg, as is remarked in Chapter XXV, says that they feed on the flowers of Freycinetias, and I have already observed that they visit the flowers of Geissois ternata in Fiji (p. 394). In this fashion Dr. Warburg regards them as agents in pollenisation ; and it seems to me that if, as appears likely, they are attracted by trees with large, brightly-coloured flowers, they would often aid in the dispersal of the minute seeds of trees like Metrosideros.

Until recently sea-birds, and some particular birds of passage, have been generally considered as only fitted for dispersing seeds in their plumage. That they can also transport seeds inside their bodies is shown below. Dr. R. Brown in his book entitled *Our Earth and its Story*, 1888, gives a general account of plant-dispersal with numerous references to the Literature on the subject. On the direct route between Scotland and Cape Farewell in Greenland snow-buntings (Plectrophanes nivalis) and other birds of passage frequently alight, as we are told, on ships when hundreds of miles from land. Dr. Brown says that when taking this voyage he examined dozens of these birds. Only in one case, however, did

he find any seeds, namely, in the case of a snow-bunting which carried, attached to its plumage, an achene of, perhaps, a Ranunculus, and in its gizzard a seed like that of a Suæda. My discovery of a small, hard seed in the gizzard of a Cape-pigeon (Daption capensis) 550 miles east of Tristan da Cunha has been referred to by Mr. Hemsley in his introduction to the *Botany of the "Challenger" Expedition* (p. 45). On p. 188 I have mentioned the probable dispersal of the seeds of Cæsalpinia by frigate-birds and boobies; and in Note 59 reference is made to some large seeds found in the crop of the Fulmar petrel.

Gulls, when they nest at the coast, where the sea-thrift (Armeria vulgaris) and the sea-campion (Silene maritima) thrive, or inland amongst the heather-covered slopes, must often carry the seeds of these plants from place to place in their plumage (see Notes 15 and 16); but, as shown below, they can also disperse plants with fleshy fruits which at times form their food. Gulls, geese, and arctic grouse take an important part in the dispersal of seeds in the cold latitudes of the northern hemisphere; and few things are more suggestive in this way to the student of distribution than the data supplied by Ekstam, Hesselman, Sernander, and others for the region including Spitzbergen, Nova Zembla, and Arctic Norway. The history of the discussion relating to the flora and fauna of Spitzbergen reproduces in its main features the various stages in the controversy that has been waged in connection with the Pacific islands.

When Ekstam published, in 1895, the results of his observations on the plants of Nova Zembla, he observed that he possessed no data to show whether swimming and wading birds fed on berries; and he attached all importance to dispersal by winds. On subsequently visiting Spitzbergen he must have been at first inclined, therefore, to the opinion of Nathorst, who, having found only a solitary species of bird (a snow-sparrow) in that region, naturally concluded that birds had been of no importance as agents in the plant-stocking. However, Ekstam's opportunities were greater, and he tells us that in the craws of six specimens of Lagopus hyperboreus shot in Spitzbergen in August he found represented almost 25 per cent. of the usual phanerogamic flora of that region, in the form of fruits, seeds, bulbils, flower-buds, leaf-buds, &c. This observer now also realised the importance of gulls and geese in dispersing certain types of plants in those latitudes. Species of Larus, he says, consume greedily all kinds of berries, and especially those of Empetrum nigrum, the stones of which were found un-

injured in their droppings by Professor Lagerheim in Arctic Norway. Geese, as we are also informed, are hearty plant-eaters in Spitzbergen; and Ekstam found in their droppings the fruits of Oxyria digyna as well as an abundance of uninjured bulbils of Polygonum viviparum, some of which proved to be capable of growth (See Ekstam in *Tromso Museums Aarshefter*, vols. 18 and 20, 1895-7).

The result of Ekstam's observations in Spitzbergen was to lead him to attach a very considerable importance in plant-dispersal to the agency of birds; and when in explanation of the Scandinavian elements in the Spitzbergen flora he had to choose between a former land connection and the agency of birds, he preferred the bird.

I have gone into some detail in this matter because the Spitzbergen controversy in some respects might have equally centred around New Zealand or some of the large continental islands of the tropical Pacific. There is at first the endeavour in the absence of precise knowledge to disregard the bird and to look for a land connection. With the increase in our acquaintance with the efficacy of bird-agency in seed distribution there is the abandonment of such a view. In both localities, however, there are the same counter-indications of the insect faunas, and the same considerations are raised by the absence or presence of larger animals in the regions concerned. The principal difference lies in the frozen sea, and yet, strangely enough, it does not seem to affect the problem much. It would indeed appear that the questions raised by the floras and faunas of the Pacific islands are not peculiarly Pacific in their character; and it is probable that the difficulties here presented are repeated in one form or other in the case of large islands over all the globe.

On the efficacy of Ducks and other Waterfowl in the Distribution of Aquatic Plants.—It is highly probable that aquatic plants, like the beach plants distributed by the currents and the ferns and lycopods distributed mainly by the winds, have changed much less in the course of ages than the plants of the inland forest. This in all three cases is chiefly due to the uninterrupted freedom of communication by means of the dispersing agency.

Wild ducks and their kind are active agents in the distribution of the seeds of aquatic plants; but it is curious that the early experiments of Caspary went far to discredit them in this respect. As quoted by Dr. Schenck in his *Die Biologie der Wassergewächse*, 1886, he fed tame ducks with the seeds of water-lilies and found

that in a short time they thoroughly digested the seeds. Those familiar with the seeds of our British species of Nuphar and Nymphæa will not be surprised at such a result; but, unfortunately, the inference drawn from this experiment has been by some extended to aquatic plants in general. Since the seeds or seed-vessels of some aquatic or semi-aquatic plants of the genera Potamogeton, Sparganium, &c., appeared to me to be quite fitted for conveyance without injury in a duck's body, I made several years ago a number of observations on this subject, the results of which were published in *Science Gossip* for September, 1894.

Out of 13 wild ducks obtained in the London market and stated to have been sent from Norfolk and Holland, eleven contained in their stomach and intestines 828 seeds, which I thus classed:—

295	seeds of Sparganium	in 8	birds
41	„ „ Potamogeton	„ 3	„
270	„ „ Cyperaceæ	„ 5	„
222	not identified		

In the case of four birds the germinating capacity of the seeds was tested, and in three cases very successfully. The seeds of Potamogeton, Sparganium, and of the Cyperaceæ germinated readily in water, but few of them failing, the process beginning in a few days or a few weeks. At that time I was conducting an extended series of observations on the postponement of germination of the seeds of aquatic plants, the results of which were published in the *Proceedings of the Royal Physical Society of Edinburgh* for 1897. It was there shown that the seeds of these plants often postpone their germination to the second and even to the third spring. It thus happened that, whilst seeds obtained from the stomach and intestines of the wild duck germinated in a few days or weeks, I had to wait often a year and more for such a result with seeds in their ordinary condition. This was well brought out in another experiment made on a domestic duck, which I have described on page 369. That wild ducks are to be regarded in the light of "flying germinators" is thus very evident.

Summary.

(1) In explanation of the shifting of the source of the Polynesian plants from the New to the Old World, it is suggested that during the glaciation of the northern hemisphere the Indo-Malayan plants entering this region were "cornered" in the tropical Western

Pacific, and were only set free after the cold period had passed away, when they overran Polynesia.

(2) Whilst the age of the Conifers is placed in the Mesozoic period, that of the Compositæ is accredited to the Tertiary period, and the era of Malayan immigration followed the glacial epoch.

(3) The suspension to a great extent of the agencies of plant-dispersal in the Pacific in later times is connected with a general principle affecting the whole plant-world. With the secular drying up of the globe the differentiation of climate, bird, and plant have gone on together, the range of the bird being mainly controlled by the climate and the range of the plant being largely dependent on the bird.

(4) Accepting Hawaii as entirely insular in its history, it is pointed out that the principles deducible from the study of its flora can be applied to the forest-flora of New Zealand, with the exception of the Conifers and some genera that are ancient denizens of Antarctic latitudes, and indicate a remote continental age dating back to the Mesozoic period. It is suggested that the Indo-Malayan element in its flora arrived there during the glaciation of the northern hemisphere.

(5) Insects and bats have probably been effective agents in seed-dispersal in the Pacific, and it is shown that sea-birds carry seeds in their stomach and intestines as well as in their feathers.

(6) It is shown that birds of the grouse family, gulls, and geese are active seed-dispersers in cold northern latitudes, and that the discussion of their influence in stocking Spitzbergen with its plants reproduces many of the points of the controversy concerning the floras of the continental islands of the South Pacific.

(7) The results of experiments and observations are cited to establish the efficacy of ducks in distributing the seeds of aquatic plants, the seeds ejected in their droppings germinating in a few days or weeks, whilst those remaining in the pond or river often do not germinate for a year or more.

CHAPTER XXXIV

GENERAL ARGUMENT AND CONCLUSION

THE problems concerned in the study of the floras of the Pacific islands from the standpoint of dispersal are here approached through the buoyant quality of the seed and fruit; and it is shown when dividing the plants into two groups, those with buoyant and those with non-buoyant seeds or fruits, that there has been at work through the ages a great sorting process, by which the plants belonging to the group first named have been mostly gathered at the coast. Its operation may be also observed within the limits of a genus, where the species possessing seeds or fruits that float is stationed at the coast, whilst the species with seeds or fruits that sink makes its home inland.

When the principle here involved is applied to the British flora, it presents itself as part of a much wider principle, by which plants endowed with buoyant seeds and fruits have been stationed at the water-side, whether on a river-bank, or beside a lake or pond, or on a sea-beach. The broader principle proves in its turn to belong to a far larger scheme, in which the fitness or unfitness of a plant to live in a physiologically dry station appears as the primary determining quality, the xerophyte (the plant of the dry station), provided with buoyant seed or fruit, finding its way to the coast, and the hygrophyte (the plant growing under more moist conditions), that is similarly endowed, establishing itself by the side of the river, or the lake, or the pond.

When dealing with the general character and composition of the strand-plants of the tropical Pacific, it is shown that in Fiji the beach-plants often assert their primary xerophilous habit or fitness for occupying any dry station by extending into the inland plains on the dry sides of the islands. The Fijian shore-plants are divided into three formations, those of the beach, those of the

mangrove-swamp, and those of intermediate stations on the borders of the swamps. The great majority of the Fijian shore-plants are dispersed by the currents. The Tahitian Islands, which are representative of Eastern Polynesia, lack the mangroves and most of the plants that grow at the margin of a mangrove-swamp; and their strand-flora is mainly composed of plants of the beach, such as are dispersed by the currents far and wide in tropical regions. The Hawaiian strand-flora is very meagre in its character, lacking not only the plants of the mangrove and intermediate formations, but almost all the large-fruited beach-trees of the South Pacific. Since Hawaii possesses but few current-dispersed shore-plants that are not found in the New World, reasons are given for the inference that such shore-plants were originally brought by the currents from America, and not from the South Pacific.

We are led on various grounds to the conclusion that tropical shore-plants distributed by currents belong to two great regions, the American including the west coast of Africa, and the Asiatic, or Old World Region, which includes the African east coast. It is held that America is so placed with regard to the currents, that it is a distributor, and not a recipient of tropical shore-plants dispersed by that agency. From this it follows that all cosmopolitan tropical beach-plants that are dispersed by the currents have their homes in America.

The results of observation and experiment are given to show that there is no direct relation between the specific weight of seeds and fruits and the density of sea-water. Yet, although the floating or sinking of a seed or fruit is but an accidental attribute, it has had indirectly a far-reaching influence not only on plant-distribution, but on plant-development. In accordance with this want of relation between the specific weight of seeds and fruits and the density of sea-water, the great variety of structures concerned with buoyancy are regarded in the main, after a detailed examination of their character, as not arising from adaptation. Rather, it is urged, is buoyancy connected with structures that now serve a purpose for which they were not originally developed. Nature, it is held, has never concerned herself directly with providing means of dispersal of any sort.

In the discussion of the relation between the littoral and inland Pacific floras, it is shown, as a result of the examination of those genera possessing both shore and inland species, that they have been on the whole developed on independent lines. Two special difficulties in explaining the modes of dispersal of plants of the

Pacific islands here come into prominence. There is the Hawaiian difficulty, where with genera containing both shore and inland species only the last are found in Hawaii; and although the shore-plants are known to be dispersed by the current, the inland plants display little or no capacity for this or any other mode of dispersal. Here belong the Leguminous genera Canavalia, Erythrina, Mezoneuron, and Sophora, and the Apocynaceous genus Ochrosia; and it is assumed that the inland Hawaiian species are derived from a current-dispersed shore-plant that has since disappeared from the group. The Fijian difficulty is displayed in those genera where both coast and inland species occur in the islands, but no known existing means of dispersal across an ocean can be postulated for the inland plants, though the shore species are distributed by the currents. Of such genera Pandanus is the best example, and it is pointed out that this genus presents the same difficulty in the Mascarene Islands, in which case the agency of the extinct Columbæ is invoked.

As illustrating the methods of observation and experiment employed by the author, the Leguminous shore-plants Afzelia bijuga, Cæsalpinia bonducella, and Entada scandens are discussed at length; and in the chapters on the enigmas of the Leguminosæ in the Pacific it is pointed out that the behaviour of the plants of this order is a source of much perplexity, and that they conform to no single rule of dispersal.

Coming to the inland plants of this region, the Fijian, Tahitian, and Hawaiian groups are taken as the chief centres of distribution in the Pacific. After discussing the relative sizes, the altitudes, and the climates of these three archipelagoes, it is shown that Hawaii, on account of the far greater altitude of the islands, is characterised by a special mountain flora, and that it is comparable with Fiji, and to a great extent also with Tahiti, only as regarding the plants of the levels below 4,000 or 5,000 feet.

The first era of the plant-stocking is designated the Age of Ferns, and it is observed that, whilst in Hawaii nearly half of the ferns and lycopods are peculiar to that group, very few new species have been developed in the Fijian and Tahitian regions.

The next era in the floral history of these islands is represented in the first era of the flowering plants. This is indicated by the endemic genera, which are particularly numerous in Hawaii, relatively scanty in Fiji, and very few in Tahiti. On account of their preponderance, the era is designated the Age of Compositæ and Lobeliaceæ. The genera of these two orders, though mainly

characteristic of Hawaii, are also to be found in the Tahitian region, but they are absent from the Fijian area. Chiefly American in their affinities, their dispersion over the Pacific took place during the Tertiary submergence of the archipelagoes of the Western Pacific, in which are included the groups of the Fijian area (Fiji, Samoa, Tonga). These early forms of Compositæ and Lobeliaceæ are often arborescent in habit; and it is observed that Tree-Lobelias also occur high up the slopes of lofty mountains in tropical regions, as in Equatorial Africa, under conditions similar to those prevailing on the slopes of the Hawaiian mountains, where the Tree-Lobelias, termed by Dr. Hillebrand "the pride of our flora," abound.

The other Hawaiian endemic genera, marking the first chapter in the history of the flowering plants, arrange themselves in two groups, one chiefly American in general affinities, and containing highly differentiated Caryophyllaceæ, Labiatæ, &c.; the other largely Malayan, and indicating the close of the first era of the flowering plants, when the main source of the plants was shifted from America to the Old World. The Fijian endemic genera, which are few in number, miscellaneous in appearance, and disconnected in character, are regarded as having probably acquired their endemic reputation through their failure at their sources in the regions to the west.

The second era of the flowering plants is indicated by the non-endemic genera. Here we are concerned on the one hand with a mountainous flora mainly Hawaiian, in which genera from the New Zealand and Antarctic floras take a conspicuous part, and on the other with a low-level flora chiefly derived from Indo-Malaya, and including the plants of the lower slopes of Hawaii below 4,000 and 5,000 feet, and the floras in mass of Fiji and Tahiti.

On account of their lower altitude, the extensive mountain flora of Hawaii is but scantily developed in Tahiti, and is represented by a mere remnant in Fiji and Samoa. Two-thirds of the Hawaiian non-endemic mountain genera contain only species restricted to the group, and, although amongst these disconnected genera, Acæna, Gunnera, Coprosma, Lagenophora, &c., of the New Zealand and Antarctic floras take a prominent part, a large proportion of the genera like Ranunculus, Rubus, Artemisia, Vaccinium, and Plantago represent generally the flora of the north temperate zone on the summits of tropical mountains. The Tahitian mountain flora, scanty as it is when judged by

the non-endemic genera, displays much kinship with the Hawaiian mountain flora; but this kinship is mainly confined to genera from high southern latitudes, such as Coprosma, Cyathodes, Astelia, &c. In the possession on its mountain slopes of the three genera of the Coniferæ, Dammara, Podocarpus, and Dacrydium, the Fijian region is distinguished from that of Tahiti and Hawaii; and it is assumed that they mark the site of a continental area in the Mesozoic period, when the Tahitian and Hawaiian groups did not exist.

The era of the non-endemic genera, in so far as it is concerned with the low-level flora of Hawaii and the floras in mass of the areas of Fiji, Samoa and East Polynesia, is termed Malayan, because many of the genera are thence derived. Here we are dealing with all the oceanic groups of the tropical Pacific, and not with a portion of them, as in the case of the Age of Coniferæ, in the Secondary period, that was limited to the Western Pacific, or in the case of the Age of Compositæ and Lobeliaceæ that was restricted during the Tertiary epoch to the Hawaiian and Tahitian regions. The first part of this era, as is indicated by the endemic species, is an age of complete isolation in Hawaii, and of partial isolation in the groups of the southern region. Amongst the genera typical of this period are Pittosporum, Gardenia, Psychotria, Cyrtandra, and Freycinetia. A later period in this era of the general dispersal of Malayan plants over the Pacific is one where the extremely variable or polymorphous species plays a conspicuous part, as represented in such genera as Alphitonia, Dodonæa, Metrosideros, Pisonia, and Wikstrœmia, the general principle being that each genus is at first represented by a widely ranging very variable species, which ultimately ceases to wander and settles down, and becomes the parent of different sets of species in the several groups.

The facts of distribution in this age of general dispersion are just such as we might look for in the case of a general dispersal over the oceanic groups of the Pacific, with the altitudes of the islands playing a determining part. But it should be remarked that the greater number of the genera that have entered the Pacific from the Old World have not advanced eastward of the Fijian region, half of the Fijian genera not occurring in the Hawaiian and Tahitian regions. The explanation of this is to be found, not in any lack of capacities for dispersal, but in a want of opportunities. The story of plant-distribution in the Pacific is bound up with the successive stages of decreasing activity in the dispers-

ing agencies. The area of active dispersion, as illustrated by the non-endemic genera, at first comprised the whole of the tropical Pacific. It was afterwards restricted to the South Pacific, and finally to the Western Pacific only. The birds that carried seeds all over this ocean became more and more restricted in their ranges, probably on account of increasing diversity of climatic conditions. The plants of necessity responded to the ever narrowing conditions of bird-life in this ocean, and the differentiation of the plant and the bird have taken place together.

During the stages of decreasing activity in the dispersing agencies, the widely-ranging highly variable species continued to be an important factor in the development of new species in the different groups. The *rôle* of the polymorphous species has always been a conspicuous one in the Pacific.

Yet, as in the case of the Cyrtandras, it is shown that the display of great formative power within a genus is not a peculiarity of an insular flora; that the isolation of an oceanic archipelago does not exclusively induce "endemism," but only intensifies it; that the development of new species may be nearly as active on a mountain in a continent as on an island in mid-ocean; and that this is equally true of a land genus, like Embelia, exposed to an infinite variety of conditions, and of an aquatic genus, like Naias, where the conditions of existence are relatively uniform all the world over.

In framing a scheme by which the eras of the floral history of the Pacific are brought into correlation with those of geological time, the age of the Coniferæ is placed in the Secondary period, that of the Compositæ and Lobeliaceæ in the Tertiary period, whilst the era of Malayan immigration is regarded as mainly post-glacial. The age of the Coniferæ is concerned only with the Western Pacific, since the Hawaiian and Tahitian islands had not then been formed. The age of the Compositæ and Lobeliaceæ is concerned only with Hawaii and Tahiti, since the islands of the Western Pacific were then more or less submerged. That of the Malayan plants affects the whole Pacific as at present displayed to us.

In the chapter on the viviparous mangroves of Fiji it is shown that both the Asiatic and the American species of Rhizophora (R. mucronata and R. mangle) exist in that group, and that there is in addition a seedless form, the Selala, which, although intermediate in character between the two other species, comes nearest to the Asiatic plant. Reasons are given for the belief that the

Selala is derived from the Asiatic species (R. mucronata), not as the result of a cross but as connected with its dimorphism; and in support of this it is pointed out that on the Ecuador coast of South America, where only the American species exists, a dimorphism is also displayed, one of the forms approaching in several of its characters the Fijian Selala, though fruiting abundantly and bearing the impress of a closer connection with the typical American species than with the Asiatic plant. The view that Rhizophora mangle reached the Western Pacific from America is rejected, and it is considered that this species was originally as widely diffused in the Old World as in America, and that it now survives only in a few places in the tropics of the Old World. The results of detailed observations on the modes of dispersal and on the germinating process both with Rhizophora and Bruguiera are given; and the absence, as a general rule, of any period of rest between the fecundation of the ovule and the germination of the seed is established.

A special chapter is devoted to the significance of vivipary, and it is considered that a record of the history of vivipary on the globe is afforded in the scale of germinative capacity that begins with the seedling hanging from a mangrove and ends with the seed that is detached in an immature condition from an inland plant. It is suggested that with the drying up of the planet in the course of ages the viviparous habit, which was once nearly universal, has been for the most part lost except in the mangrove swamp, which to some extent represents an age when the earth was enveloped in cloud and mist and the atmosphere was saturated with aqueous vapour. The lost habit is at times revived in the abnormal vivipary of some inland plants, and traces of it are seen in the abnormal structure of the seeds of some genera of the Myrtaceæ, like Barringtonia, and in the seeds of genera of other orders. With the desiccation of the planet and the emergence of the continents there has been continual differentiation of climate resulting in seasonal variation and in the development of the rest-period of the seed.

With the secular drying of the globe and the consequent differentiation of climate is to be connected the suspension to a great extent of the agency of birds as plant-dispersers in later ages, not only in the Pacific Islands but over all the tropics. The changes of climate, bird, and plant have gone on together, the range of the bird being controlled by the climate, and the distribution of the plant being largely dependent on the bird.

The history of climate, the history of the continents and of the oceans, the history of life itself, but only in the sense below defined, all belong to that of a desiccating world, or rather of a planet once sunless and enveloped in mist and cloud, that through the ages has been drying up. Life's types were few and the sea prevailed, and one climate reigned over the globe. With the diminution of the aqueous envelopes the continents began to emerge, climates began to individualise, and organisms commenced to differentiate, and thus the process has run on through the past, ever from the general to the special both in the organic and in the inorganic world.

The same story of a world drying up is told by the marine remains left stranded far up some mountain slope, or by the bird akin to no other of its kind that Time has stranded on some island in mid-Pacific. The bird generalised in type that once ranged the globe is now represented over its original range by a hundred different groups of descendants, confined each to its own locality. Climate, once so uniform, now so diversified, has by restricting the range of the bird favoured the process of differentiation, and the plant dependent on the bird for its distribution has in its turn responded to these changes.

The *rôle* of the polymorphous species belongs alike to the plant and to the bird. A species that covers the range of a genus varies at first in every region and ultimately gives birth to new species in some parts of its range. Then the wide-ranging species disappears and the original area is divided up into a number of smaller areas each with its own group of species. Each smaller area breaks up again, and forms, yet more specialised, are produced ; and thus the process of subdivision of range and of differentiation of form goes along until each island in an archipelago owns its bird and each hill and valley has its separate plants. This is not the path that Evolution takes, since beyond lies extinction whether of plant or of bird. Such is the upshot of the process of differentiation exhibited in the development of species and genera in the Pacific Islands, or, indeed, in any oceanic groups. It can never do more than produce a Dodo or a Kiwi, or amongst the plants a Tree-Lobelia.

Evolution here and elsewhere is a thing apart from species and genera, which are but eddies on the surface of its stream. It is a scheme of life introduced into a much conditioned world, and adaptation in endless forms is the price it has had to pay. The whole story of life on this earth is a story of a sacrifice, of an end to be won, but of a price to be paid. Immortality is in the

scheme, but death is the price of adaptation. The same theme runs through our conceptions of the spiritual life. There is the same duality, evolution adapting its scheme to the exigencies of the physical world, the good principle ever in conflict with the evil, and at times compelled to adapt itself to attain its ends. There is the tale of adaptation in the one case and of sacrifice in the other, and success is reached in both.

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NOTE 1 (page 13)

On the Number of Known Species of Fijian Flowering Plants

Rather over 600 species of flowering plants are included in Seemann's *Flora Vitiensis*, excluding the weeds and the plants introduced by man. Horne's collections would probably add another 300 species; and many more remain to be discovered.

NOTE 2 (page 13)

The Littoral Plants of Fiji

In the following table are incorporated the results of an extensive series of observations and experiments on the buoyancy of the seeds and fruits of the shore plants made by the author during his sojourn of two years in Fiji, and based not only on prolonged buoyancy-tests, but also on systematic examination of the stranded and floating seed-drift, both of sea and river. The details would occupy many chapters: and it is only possible here to give the bare results. Since Professor Schimper went over much the same ground in the Malayan region, one enjoys in many cases the great advantage of his authority; but a fair proportion of the results are new; and, besides, there are a number of plants included, the buoyancy of whose seeds or fruits has long been well established. In all cases the seed or fruit is taken as it presents itself for dispersal by the currents. Many of the plants are discussed with some detail in various parts of this book, as indicated in the reference column of the table.

Since the Gramineæ and the Cyperaceæ contain very few species suited for direct transport by the currents over wide areas of sea, this list may be regarded as containing nearly all the littoral flowering plants possessing seeds or seed-vessels with any buoyancy of importance.

Nearly all the Tahitian strictly littoral plants are represented in Fiji, and the few that have not been found there yet, such as Sesbania grandiflora, Heliotropium anomalum, &c., may exist, as in the first-named species, in the neighbouring Tongan group, and may probably even exist in Fiji. Two other Tahitian littoral plants, that are widely spread in the Pacific, namely, Suriana maritima and Sesuvium Portulacastrum, are found in Tonga, and are included in my list of Fijian shore plants, though not yet recorded from that group, where, however, they will, without a doubt, be found by some future observer.

Table showing the Buoyancy of the Seeds or Fruits of the Littoral Plants of Fiji, excluding the Grasses and, with one exception, the Sedges

The letters placed before the plant name indicate that the species is also found in Hawaii (H), in Tahiti (T), and in the Marquesas (M). The Marquesan locality is only given where the plant is not in Tahiti.

The abbreviations in the reference column are as follows:

S=Schimper; G=Guppy; P=Earlier authorities and particularly the list given by Hemsley in the Introduction to the *Botany of the Challenger Expedition.*

Species.	Family.	Buoyancy of seeds or fruits.		Authorities.	Pages of further reference. See also Index.
		Float for months.	Sink at once or in a week or two.		
HT Calophyllum inophyllum	Guttiferæ.	+	...	S. G. P.	18
HT Hibiscus tiliaceus	Malvaceæ.	+	...	S. G. P.	21
Hibiscus diversifolius (Jacq.)	,,	+	...	G.	21
HT Thespesia populnea	,,	+	...	S. G. P.	Note 3
H Gossypium tomentosum (Nutt.)	,,	...	+	G.	
Heritiera littoralis	Sterculiaceæ.	+	...	S. G. P.	45, 48
T Kleinhovia hospita	,,	+	...	G.	21
T Triumfetta rhomboidea	Tiliaceæ.	...	+ ?		
T Triumfetta procumbens	,,	...	+	G.	45
T Suriana maritima	Simarubeæ.	+	...	S. G.	
Carapa moluccensis	Meliaceæ.	+	...	S. G. P.	45
Carapa obovata	,,	+	...	S. G. P.	45
T Ximenia americana	Olacineæ.	+	...	S. G.	113
Smythea pacifica (Seem.)	Rhamneæ.	+	...	G. P.	106
HT Colubrina asiatica	,,	+	...	G.	137
HT Dodonæa viscosa	Sapindaceæ.	+	...	S. G.	
HT Tephrosia piscatoria	Papilionaceæ.	...	+	G.	45
M Desmodium umbellatum	,,	...	+	G.	
HT Dioclea violacea	,,	+	...	G. P.	82
T Canavalia obtusifolia	,,	+	...	S. G. P.	Note 54
T Canavalia sericea	,,	+	...	G.	Note 54
T Canavalia ensiformis, var. turgida.	,,	+	...	S. G. P. ?	Note 54
HT Mucuna gigantea	,,	+	...	S. G. P.	81
T Erythrina indica	,,	+	...	S. G. P.	
HT Strongylodon lucidum	,,	+	...	G.	82
HT Vigna lutea	,,	+	...	S. G.	139
Dalbergia monosperma	,,	+	...	S. G.	106
Derris uliginosa	,,	+	...	S. G. P.	111
Pongamia glabra	,,	+	...	S. G. P.	
T Sophora tomentosa	,,	+	...	S. G.	Note 56
T Inocarpus edulis	,,	+ ?	...	G. P.	
HT Cæsalpinia Bonducella	Cæsalpinieæ.	+	...	S. G. P.	193
T Cæsalpinia Bonduc	,,	+	...	G. P.	193
Afzelia bijuga	,,	+	...	G.	173
Cynometra sp.	,,	+ ?	...	S. G.	
Entada scandens	Mimoseæ.	+	...	G. P.	181
Acacia laurifolia	,,	...	+	G.	164
T Leucæna Forsteri	,,	...	+	G.	
T Serianthes myriadenia	,,	...	+	G.	424
Parinarium laurinum	Rosaceæ.	+	...	G. P.	
Eugenia Richii	Myrtaceæ.	...	+	G.	
T Barringtonia speciosa	,,	+	...	S. G. P.	
Barringtonia racemosa	,,	+	...	G.	
Rhizophora mucronata	Rhizophoreæ.	+	...	S. G. P.	
Rhizophora mangle	,,	+	...	S. G. P.	
Bruguiera Rheedii	,,	+	...	G. P.	
HT Terminalia Katappa	Combretaceæ.	+	...	S. G. P.	
M Terminalia littoralis	,,	+	...	S. G. P.	
Lumnitzera coccinea	,,	+	...	S. G. P.	
T Gyrocarpus Jacquini	,,	+	...	G.	423
T Pemphis acidula	Lythraceæ.	+	...	S. G.	
T Luffa insularum (Gray)	Cucurbitaceæ.	+	...	G.	426
HT Sesuvium Portulacastrum	Ficoideæ.	...	+	G.	
HT Morinda citrifolia	Rubiaceæ.	+	...	S. G. P.	
T Guettarda speciosa	,,	+	...	S. G. P	
T Wedelia biflora	Compositæ.	+	...	G.	
HT Scævola Koenigii	Goodeniaceæ.	+	...	S. G. P.	

TABLE SHOWING THE BUOYANCY OF THE SEEDS OR FRUITS OF THE LITTORAL PLANTS OF FIJI, EXCLUDING THE GRASSES, AND WITH ONE EXCEPTION, THE SEDGES (*continued*)

Species.	Family.	Buoyancy of seeds or fruits. Float for months.	Buoyancy of seeds or fruits. Sink at once or in a week or two.	Authorities.	Pages of further reference. See also Index.
T Cerbera Odollam	Apocynaceæ.	+	...	S. G. P.	
T Ochrosia parviflora	,,	+	...	G. P.	
HT Cordia subcordata	Boraginaceæ.	+	...	S. G. P.	
T Tournefortia argentea	,,	+	...	S. G. P.	
HT Ipomea pes capræ	Convolvulaceæ.	+	...	S. G. P.	
H Ipomea glaberrima (Boj.)	,,	+	...	G.	
Aniseia uniflora	,,	+	...	G.	
T Premna tahitensis	Verbenaceæ.	+	...	G.	Note 32
Clerodendron inerme	,,	+	...	S. G.	
HM Vitex trifolia	,,	+	...	G.	
HT Cassytha filiformis	Lauraceæ.	+	...	G.	
T Hernandia peltata	,,	+	...	S. G.	
HT Wikstrœmia fœtida	Thymelæaceæ.	...	+	G.	
Drymispermum Burnettianum	,,	...	+	G.	
T Euphorbia Atoto	Euphorbiaceæ.	...	+	S. P. G.	
Excæcaria Agallocha	,,	+	...	S. G.	
T Casuarina equisetifolia	Casuarineæ.	...	+	G.	
HT Tacca pinnatifida	Taccaceæ.	+	...	G.	19
HT Cocos nucifera	Palmeæ.	+	...	P.	
HT Pandanus odoratissimus	Pandaneæ.	+	...	S. G. P.	
Crinum asiaticum	Amaryllideæ.	...	+	G. P.	
Scirpodendron costatum	Cyperaceæ.	+	...	G.	407
Cycas circinalis	Cycadeæ.	+	...	G. P.	

NOTE 3. (page 13)

RESULTS OF LONG FLOTATION EXPERIMENTS ON THE SEEDS OR SEED-VESSELS OF TROPICAL LITTORAL PLANTS

At various times during the past twenty years I have made lengthened experiments in England on the buoyancy in sea-water of the seeds or seed-vessels of beach plants collected by me in the Solomon Islands, the Fijis, Hawaii, Keeling Atoll, &c. In all the species enumerated below, the floating powers were retained after twelve months' immersion, the seed-contents being to all appearance unharmed. In six species I succeeded in getting the seeds to germinate after the experiment; and there can be no doubt that the number of successful results would have been largely increased, if I had not been obliged to resort to very primitive methods in conducting the experiments. Some of the results are referred to in a note to my paper on the flora of Keeling Atoll, dated about 1889; and if I remember aright, Mr. Hemsley mentioned those relating to Thespesia populnea and Ipomea grandiflora in the *Annals of Botany*, not long after. The others have not been previously published. In one instance (Cæsalpinia bonducella) the flotation experiment was prolonged to two and a half years, the seeds floating buoyantly and being apparently quite sound at the end of the experiment.

As demonstrating that tropical seeds can be transported unharmed by currents through cold latitudes, it should be noted that all these experiments were conducted in England. In the cases of the Keeling Atoll seeds the experiment was carried on through a very severe winter, the vessel of sea-water being exposed to a degree of cold that kept fresh-water frozen for three weeks on the same table. This did not prevent the subsequent germination of the seeds of Thespesia populnea and Ipomea grandiflora. The same thing was established in a more natural way by Lindman, who planted seeds of Entada scandens and Mucuna urens, that had been stranded on the Norwegian coast, and found that they retained their germinating capacity (see Sernander, p. 7).

The following are the seeds or seed-vessels that remained afloat after a year's flotation in sea-water, those that subsequently germinated being preceded by G. In the other cases the germinating capacity was not tested; but they were always sound in appearance when cut across at the close of the experiment.

G Thespesia populnea (Malvaceæ)
Dioclea (violacea?) (Papilionaceæ)
G Mucuna gigantea, D C ,,
G Mucuna urens, D C ,,
Mucuna, sp. ,,
Mucuna, sp. ,,
G Strongylodon lucidum, Seem. ,,
Sophora tomentosa, ,,
G Cæsalpinia bonducella (Cæsalpinieæ)
Entada scandens (Mimoseæ)
Morinda citrifolia (Rubiaceæ)
Scævola Koenigii (Goodeniaceæ)
Cordia subcordata (Boragineæ)
Tournefortia argentea ,,
G Ipomea grandiflora, Lam. (Convolvulaceæ)
Tacca pinnatifida (Taccaceæ)

NOTE 4 (page 13)

Table illustrating the Degree of Buoyancy of the Seeds and Fruits of Inland Fijian Plants

(Unless otherwise indicated, the seeds or fruits sink at once or in a day or two)

✓Abrus precatorius.
Acacia Richii.
✓Ageratum conyzoides.
Alphitonia excelsa.
Alpinia sp.
Alyxia (scandens?).
Artocarpus incisa.
,, integrifolia.
Barringtonia edulis (1 month)
,, sp.
Bauhinia sp.
Bischoffia javanica.
Cæsalpinia sp.
Calophyllum spectabile (2-4 weeks).
,, Burmanni (4-10 days).
Cananga odorata.

TABLE ILLUSTRATING THE DEGREE OF BUOYANCY OF THE SEEDS AND FRUITS OF INLAND FIJIAN PLANTS (*continued*)

Canarium sp.
,, sp.
Canna indica.
Citrus aurantium (3-4 weeks).
,, decumana (1 month).
,, limonum (5 weeks).
,, vulgaris, R. (6-7 weeks).
Coix lachryma (2-7 days).
Commersonia platyphylla.
Cordyline sepiaria.
Couthovia corynocarpa (a few days).
Cucumis acidus (a few days).
Cucurbita sp. (several months).
Cupania sp.
Dammara vitiensis (7-10 days).
Dioscorea sativa (a few days).
,, sp.
Dracontomelon sylvestre.
,, sp.
Elæocarpus sp.
,, sp. (a few days).
Eranthemum sp.
Eugenia malaccensis (2-4 weeks).
,, effusa? (4-7 days).
,, confertiflora? (10-12 days).
,, rariflora (a few days).
,, corynocarpa (a few days).
,, rivularis (a week).
Fagræa Berteriana (a few days).
Ficus Harveyi, ,, scabra, ,, sp. } (7-10 days).
Gardenia vitiensis (4-5 weeks).
Geissois ternata.
Geophila reniformis.
Gnetum gnemon.
Grewia sp.
Guettarda sp. (a few weeks).
Hibiscus Abelmoschus (months).
,, seculentus.
Hydrocotyle asiatica (months).
Ipomea batatas.
,, insularis (*nil* or months).
,, peltata (weeks or months).
Ipomea turpethum (*nil* or weeks or months).
,, sp. (7-10 days).
Lindenia vitiensis (weeks or months).
Maba sp. (7-10 days).
Macaranga sp. (1-2 weeks).
Melastoma denticulatum.
Micromelum minutum.
Momordica Charantia (a few days).
Morinda Forsteri.
Mussænda frondosa.
Myristica sp., ,, sp. } (3-7 days).
Myrmecodia sp.
Nelitris vitiensis (a few days).
Nephelium pinnatum (a few days).
Ophiorrhiza leptantha.
Phyllanthus sp.
,, sp.
Piper Macgillivrayi.
Pittosporum sp.
Pleiosmilax vitiensis.
Portulaca (lutea ?).
,, quadrifida.
Premna serratifolia.
Pritchardia pacifica.
Psychotria sp.
,, sp.
,, sp.
,, sp.
,, sp.
Ptychosperma sp.
Rhaphidophora vitiensis.
Sapota sp., ,, sp. } (a few days).
Scævola floribunda.
Spondias dulcis (a month).
Sterculia sp. (seeds *nil*, fruits months).
Stylocoryne sambucina (2 or 3 days).
Tabernæmontana (orientalis ?) (a few days).
Tacca maculata (*nil* or a few days).
Trichospermum Richii (a few days).
Urena lobata.
Veitchia Joannis.
,, sp.

NOTE 5 (page 14).

THE INLAND FIJIAN PLANTS POSSESSING BUOYANT SEEDS OR FRUITS

They come under the following heads:—

(a) Plants of the stream-border or the pond-side or of the inland swamp, *e.g.*, Lindenia vitiensis and Hydrocotyle asiatica. The extension of the principle by which plants with buoyant seeds or fruits are located, not only at the sea-side but at the water-side generally, is here involved, as explained in Chapter III.

(b) Plants following the rule deduced by Schimper for Terminalia, that when a genus comprises several species possessing buoyant fruits, only those having fruits with the greatest floating power are found at the coast, the least buoyant plants occurring inland; examples, Calophyllum and Guettarda.

(c) Plants that like Ipomea behave irregularly in respect to seed-buoyancy, a difference in behaviour often associated with varying stations both at the coast and inland.

(d) Plants with dehiscent buoyant capsular fruits, like Sterculia, where dehiscence takes place on the tree and the seeds have no buoyancy. Although the unopened fruit may float a long time, it does not in that condition come under the influence of the currents.

(e) Plants like Citrus Decumana, Gardenia, sp., &c., that, although apparently exceptions to the principle, do not offer much opposition to it, since the first is most at home at the river-side and the second often displays a decided inclination for a station at the coast.

(f) Genuine exceptions to the principle, such as Hibiscus Abelmoschus (see page 21).

NOTE 6 (page 15)

Table showing the Degree of Buoyancy of the Seeds and Fruits of some Inland Hawaiian Plants

(Unless otherwise stated, the seeds or fruits sink at once or in a day or two)

Acacia Koa.
Aleurites moluccana (1–2 weeks).
Alyxia olivæformis.
Argemone mexicana.
Argyreia tiliæfolia (*nil* or months).
Bidens pilosa.
Campylotheca sp.
Canavalia galeata.
Capparis sandwicensis.
Cassia Gaudichaudii.
,, occidentalis.
Cheirodendron Gaudichaudii.
Colubrina oppositifolia (weeks).
Commelyne nudiflora.
Coprosma ernodeoides.
,, sp.
,, sp.
Cyathodes Tameiameiæ (a few days).
Cyrtandra sp. ⎫
,, sp. ⎬ (a few days).
,, sp. ⎭
Dianella odorata (a few days).
Dracæna aurea.
Eclipta alba (months).
Erythrina monosperma.
Gossypium tomentosum (a week).
,, barbadense (a few days).
,, sp. cultiv. (a few days).
Hibiscus Youngianus (weeks).
Hydrocotyle verticillata (weeks).
Ipomea bona nox (*nil* or months).
,, insularis.
,, pentaphylla.
,, reptans.
,, tuberculata.
Jacquemontia sandwicensis.
Jussiæa villosa (a few days).
Lobeliaceæ (Clermontia).
Maba sandwicensis.
Metrosideros polymorpha.
Mezoneuron kauaiense (pod, a week).
Mucuna urens (months).
Myoporum sandwicense.
Olea sandwicensis, see page 364.
Phyllostegia grandiflora.
,, mollis.
Plectronia odorata.
Pritchardia Gaudichaudii (5 or 6 weeks).
Ricinus communis (7–10 days).
Rubus Macraei.
Scævola Chamissoniana.
,, Gaudichaudii.
Sida fallax.
Sisyrinchium acre.
Solanum aculeatissimum.
Sophora chrysophylla (pod, 1–2 weeks).
Viola Chamissoniana.
Waltheria americana.

NOTE 7 (page 15)

Some Inland Hawaiian Plants possessing Buoyant Seeds or Fruits

Three of these, Eclipta alba, Hibiscus Youngianus, and Hydrocotyle verticillata, frequent wet places, and come under the principle that water-side plants generally have buoyant seeds or fruits. The buoyancy of the seeds of Argyreia tiliæfolia and of Ipomea bona nox varies with station and may be explained as under Ipomea in Note 5. The floating power of the fruits of Colubrina oppositifolia may be akin to that of inland species of Terminalia as indicated in Note 5, since another species of the genus C. asiatica, which is a coast plant, has very buoyant seeds. Mucuna urens was no doubt originally, as it now is in tropical America, a littoral plant. The buoyant fruits of Pritchardia Gaudichaudii offer a genuine exception to the principle (see page 330).

NOTE 8 (pages 18, 112)

The Pyrenes of Morinda

The pyrenes of the two Malayan inland species of Morinda (M. umbellata and M. longiflora) examined by Professor Schimper do not possess the bladder-like cavity to which those of M. citrifolia owe their floating power, and it is to be inferred from his remarks (p. 183) that they have little or no buoyancy. The pyrenes of a Fijian inland species, near M. Grayi, had no floating power as tested by me, and they lacked the bladder-like cavity.

NOTE 9 (page 18)

The Buoyancy of the Fruits of Calophyllum

Professor Schimper found that whilst the fruits of Calophyllum inophyllum, the shore tree, remained afloat after 126 days, those of C. amœnum, an inland species, sank in from three to fourteen days, both possessing similar buoyant structures, but to a less degree in the case of the inland species. This genus presents a parallel case to Terminalia referred to on page 17; but the general discussion of the subject will be found in Chapter XIII. According to the above authority C. Calaba, a West Indian coast tree, has buoyant fruits. The same is also true of the fruits of a large inland tree in the Solomon Islands experimented on by me (*Solomon Islands*, p. 305). It would thus appear that the fruits of the genus are as a rule buoyant, and that, as in Terminalia, the least buoyant fruits belong to the inland species. Professor Schimper also shows (p. 182) that the diminished floating power of the fruits of the inland species is associated with diminution in thickness of the buoyant seed-shell which is most developed in the buoyant fruits of the strand species.

NOTE 10 (page 24)

The Buoyancy Experiments on British Plants

The experiments in all cases were made to test the floating power of the seed or fruit in the condition in which it is detached from the plant. It usually makes very little difference whether sea-water or fresh water is employed, since in my numerous experiments there were but few exceptions to the general rule that seeds or seed-vessels that sink in fresh water sink also in sea-water. This subject is discussed in Chapter X. However, it may be here observed that the chief effect of the increased density of sea-water is merely to increase the proportion of buoyant seeds or fruits in any particular species.

It is necessary in such experiments to imitate Nature as much as possible. The seed or fruit, as the case may be, must be experimented upon in the condition in which it falls from the plant, or in the condition in which it would be ultimately found in river and pond drift. The seed or fruit should be thoroughly wetted, and air-bubbles removed.

Prolonged drying has but a slight effect on the great majority of seeds and seed-vessels experimented on, and this is just as true of tropical plants. Those that sink at once in the mature and fresh condition rarely float more than a day or two even after drying for a year. The usual effect is to increase the floating capacity of seeds and fruits already buoyant, and not to develop the capacity.

The results given in the table refer only to sound seeds. In fresh-water experiments, in nearly all cases, the seeds ultimately germinate in the water, and this is the usual cause of the close of the experiment. In an ordinary collection of floating seed drift from a pond or river, germination will go on for years at each successive spring, the postponement of germination being a very striking feature with a fair proportion of seeds in river and pond-drift. This subject is dealt with in detail in my paper published in the *Proceedings* for 1897 of the Royal Physical Society of Edinburgh.

The Table of Results of Observations and Experiments on the Buoyancy of the Seeds or Seed-vessels of more than 300 British Flowering Plants

Explanation of Table.—The capacity of floating for months is thus indicated, ++; of floating for 1 to 4 weeks, +; and where sinking occurs at once or within a week there is no entry. When buoyancy continued in my experiments after 6 and 12 months, it is indicated by Roman numerals (VI and XII). A=an aquatic plant; M=a beach plant; R=a river-side or pond-side plant; var.=variable in floating power.

R Thalictrum flavum			R Caltha palustris	+	
A Ranunculus aquatilis			Berberis vulgaris		
R ,, hederaceus			A Nymphæa alba		
R ,, flammula			A Nuphar luteum		
,, ficaria			Papaver rhœas		
R ,, sceleratus VI	++	Var.	,, dubium		
,, acris			Chelidonium majus		
,, repens XII	++	Var.	Rœmeria hybrida		

THE TABLE OF RESULTS OF OBSERVATIONS AND EXPERIMENTS ON THE BUOYANCY OF THE SEEDS OR SEED-VESSELS OF MORE THAN 300 BRITISH FLOWERING PLANTS (*continued*)

M Glaucium luteum		
Barbarea vulgaris		
R Nasturtium officinale		
R ,, sylvestre		
R ,, amphibium		
Arabis hirsuta		
,, thaliana		
R Cardamine pratensis		
,, hirsuta		
Alliaria officinalis		
Brassica campestris		
,, alba		
M Cochlearia officinalis		
M Alyssum maritimum		
Draba verna		
Thlaspi arvense		
Capsella bursa pastoris		
M Cakile maritima	+	
M Crambe maritima	+	
M Raphanus maritimus	+	
Reseda luteola		
Helianthemum vulgare		
R Viola palustris		
,, canina		
,, tricolor		
Polygala vulgaris		
Silene cucubalus		
M ,, maritima		
Lychnis diurna		
Sagina procumbens		
M Arenaria peploides (Honckeneya) XII	++	
Mœnchia erecta		
Cerastium vulgatum		
R Stellaria aquatica		
,, media		
,, graminea		
,, holostea		
Spergularia rubra		
M ,, marina		
Spergula arvensis		
R Montia fontana		
R Elatine hydropiper		
Hypericum perforatum		
,, quadrangulum		
R ,, elodes		
Linum usitatissimum		
,, angustifolium		
Malva rotundifolia		
,, sylvestris		
Oxalis acetosella		
,, corniculata		
Impatiens parviflora		
R ,, fulva VI	++	
Acer campestre		
Ilex aquifolium		
Euonymus europæus	+	
Ulex europæus		
Cytisus scoparius		
Ononis arvensis		
Medicago lupulina		
,, denticulata		
Trifolium incarnatum		
Lotus corniculatus		
Anthyllis vulneraria		
Vicia sativa		
Lathyrus pratensis		
M ,, maritimus	++	
R Spiræa ulmaria	+	
Fragaria vesca		
Potentilla tormentilla		
,, sp.		
R ,, comarum XII	++	
Alchemilla arvensis		
Rosa arvensis		
Cratægus oxyacantha	+	
R Epilobium hirsutum		
,, parviflorum		
R Lythrum salicaria		
R Peplis portula		
Bryonia dioica		
Cotyledon umbilicus		
Saxifraga granulata		
,, tridactylites		
R Chrysosplenium alternifolium		
R ,, oppositifolium		
Drosera rotundifolia	+	
A Myriophyllum spicatum		
A ,, alternifolium		
R Hydrocotyle vulgaris XII	++	
M Eryngium maritimum		
R Cicuta virosa	++	
R Apium graveolens		
R ,, nodiflorum		
R ,, inundatum		
R Sium latifolium	++	
R ,, angustifolium	++	
R Œnanthe crocata VI	++	
R ,, phellandrium	+	
Æthusa cynapium		
M Crithmum maritimum	++	
R Angelica sylvestris XII	++	
R Peucedanum palustre	++	
Pastinaca sativa		
Chærophyllum sylvestre		
Smyrnium olusatrum		
Hedera helix		
Viscum album		
Sambucus nigra		
R Galium palustre VI	++	
,, mollugo		
,, aparine		
Centranthus ruber		
Valerianella olitoria		
Eupatorium cannabinum		
M Aster tripolium		
R Bidens cernua VI	++	
R ,, tripartita VI	++	
Chrysanthemum segetum		
,, leucanthemum		
Matricaria inodora		
M ,, inodora, var. maritima	++	
,, chamomilla		
Achillea millefolium		
Artemisia vulgaris		
,, absinthium		
Tussilago farfara		
,, petasites		
Senecio vulgaris		
R ,, aquaticus		
R ,, palustris		
Carduus nutans		
,, lanceolatus		
R ,, palustris		
,, arvensis		
Tragopogon pratensis		
,, porrifolius		
,, echioides		
Leontodon autumnalis		
Sonchus oleraceus		
Taraxacum dens leonis		
Crepis virens		
,, fœtida		
Lapsana communis		
A Lobelia Dortmanna		
R Hottonia palustris		
R Lysimachia vulgaris	+	

THE TABLE OF RESULTS OF OBSERVATIONS AND EXPERIMENTS ON THE BUOYANCY OF THE SEEDS OR SEED-VESSELS OF MORE THAN 300 BRITISH FLOWERING PLANTS (*continued*)

R	Lysimachia thyrsiflora	+	
M	Glaux maritima		
	Anagallis arvensis		
M	Samolus valerandi		
	Pinguicula lusitanica		
	Ligustrum vulgare		
R	Menyanthes trifoliata	++	
R	Limnanthemum nymphæoides	+	
	Convolvulus arvensis		
	,, sepium XII	++	
M	,, soldanella XII	++	
	Cuscuta europæa		
	Lithospermum officinale		
R	Myosotis palustris		
	,, arvensis		
	,, versicolor		
	Lycopsis arvensis		
	Symphytum officinale		
	Borago officinalis		
	Datura stramonium		
	Solanum dulcamara		
	,, nigrum		
	Linaria vulgaris		
	,, cymbalaria		
	Scrophularia nodosa		
R	,, aquatica		
R	Veronica anagallis		
R	,, beccabunga		
	,, agrestis		
	,, arvensis		
	Bartsia odontites		
	Rhinanthus crista galli VI	++	Var.
R	Pedicularis palustris	++	
	Salvia verbenaca		
R	Lycopus europæus XII	++	
R	Mentha aquatica VI	++	
	Thymus sp.		
	Calamintha officinalis		
	Nepeta glechoma		
	,, cataria		
	Prunella vulgaris		
R	Scutellaria galericulata XII	++	
	Stachys betonica		
	,, sylvatica		
R	,, palustris	++	
	,, arvensis		
	Galeopsis tetrahit		
	Ballota nigra		
	Lamium purpureum		
	,, album		
	,, galeobdolon		
	Teucrium scorodonia		
	Ajuga reptans		
	Verbena officinalis		
M	Armeria vulgaris		
	Plantago major		
	,, media		
	,, lanceolata		
M	,, maritima		
M	Salicornia herbacea		
M	Salsola kali	+	
M	Suæda fruticosa		
M	,, maritima		
	Chenopodium album		
M	Beta maritima		
	Atriplex patula VI	++	
R	Rumex aquaticus	+	
	,, crispus	++	
	,, obtusifolius		
R	,, hydrolapathum XII	++	
R	,, conglomeratus XII	++	
	Polygonum aviculare		
M	,, maritimum		
	,, convolvulus		
R	Polygonum amphibium		
R	,, persicaria		
	,, lapathifolium		
R	,, hydropiper		
	Euphorbia helioscopia		
	,, segetalis		
M	,, paralias	++	
	,, peplus (?)		
	,, amygdaloides		
A	Ceratophyllum demersum		
A	Callitriche aquatica		
	Urtica dioica		
	Ulmus campestris		
R	Alnus glutinosa XII	++	
	Betula alba		
	Corylus avellana	+	
	Quercus robur	+	
	Pinus sylvestris	+	
	Taxus baccata		
R	Typha latifolia		
R	,, angustifolia		
R	Sparganium ramosum XII	++	
R	,, simplex VI	++	Var.
R	,, minimum	++	
	Arum maculatum		
R	Calla palustris XII	++	
A	Lemna minor	++	
A	,, gibba		
A	Naias marina		
A	Zannichellia palustris		
A	Ruppia maritima		
A	Potamogeton natans XII	++	
A	,, oblongus VI	++	
A	,, lucens VI	++	
A	,, perfoliatus	++	
A	,, crispus		
A	,, densus		
A	,, obtusifolius		
A	,, pusillus		
R	Butomus umbellatus		
R	Sagittaria sagittifolia VI	++	Var.
R	Alisma plantago VI	++	Var.
R	,, ranunculoides		
A	,, natans		
R	Damasonium stellatum		
R	Scheuchzeria palustris	++	
R	Triglochin palustre		
R	,, maritimum		
A	Hydrocharis morsus ranæ		
R	Iris pseudacorus XII	++	
	,, fœtidissima		
	Tamus communis		
	Fritillaria meleagris	++	
	Scilla nutans		
	Narthecium ossifragum		
R	Juncus communis		
	,, glaucus		
R	,, articulatus		
	,, squarrosus		
R	,, bufonius		
M	,, maritimus		
	Luzula campestris		
R	Cladium mariscus	++	
R	Blysmus rufus	++	
R	Scirpus palustris		
A	,, fluitans		
	,, setaceus		
	,, holoschœnus		
R	,, lacustris		
M	,, maritimus	+	
	,, sylvaticus		
	Eriophorum alpinum		
	,, vaginatum		
	,, polystachion		

THE TABLE OF RESULTS OF OBSERVATIONS AND EXPERIMENTS ON THE BUOYANCY OF THE SEEDS OR SEED-VESSELS OF MORE THAN 300 BRITISH FLOWERING PLANTS (*continued*)

R	Carex leporina	++		R	Carex ampullacea	+	
	,, stellulata XII	++		R	,, paludosa XII	++	
R	,, canescens	++			,, sp.		
	,, remota XII	++			,, sp.		
R	,, paniculata XII	++		R	Leersia oryzoides		
R	,, vulpina XII	++		R	Alopecurus geniculatus		
R	,, acuta VI	++			Agrostis sp.		
	,, hirta				,, sp.		
R	,, flava VI	++	var.	R	Poa aquatica		
	,, distans			R	,, fluitans		
	,, panicea				Melica nutans		
R	,, pseudocyperus VI	++		R	Arundo phragmites	+ ?	

Total of the original list: 320 species belonging to 192 genera and 65 families. Of these, about 260 were tested by the author, the data for the remaining species being mainly derived from the writings of Thuret, Kolpin-Ravn, and Sernander, with a few from those of Darwin and Martins.

NOTE.—Whilst this work has been going through the press, the author has added thirteen species, seven genera, and two families to the list above given; but the general inferences are not affected by the additions. The corrected total would, therefore, be 333 species, 199 genera, and 67 families.

On the effect of drying on the buoyancy of seeds and seed-vessels

It has been already observed that this is as a rule but slight, and that in the great majority of cases the effect of prolonged drying for many months, or even for years, is at the most to give a seed or fruit originally non-buoyant a floating power of a few days' duration. This is a subject to which I have paid especial attention in my experiments, since, of course, much depends on it in the way of dispersal by currents. It is obvious that a seed or fruit possessing impermeable coverings at the time of its separation from the parent can scarcely be compared with one where the coverings only attain their water-proof capacity by drying. Most gardeners know that seeds which dry easily take up moisture easily, and the principle applies in a varying degree to the great majority of seeds and fruits.

Darwin was inclined to attach importance to adventitious buoyancy acquired by drying; and in the *Origin of Species* he refers to instances offered by the fruits of the Hazel (Corylus), the Asparagus, and Helioscladium. In Note 48 I have referred to the cases of the Oak and the Hazel; and, indeed, we have only to examine the beach-drift in various parts of the world, and to look at their respective stations, to learn that this is not an effective mode of dispersal. Buoyancy of seed or fruit is only one of many other qualities that is concerned with distribution by currents. Nature does not act in this way in seed-distribution, and there can be little doubt that the author of the *Origin of Species* would have been the first to abandon this view, if his researches had been continued. It should be especially noted that plants of the sea-beach, where the floating power happens to be *nil*, or limited only to a week or two, would have derived great advantage from the drying of their seeds or fruits if it was really effective in aiding dispersal by currents. However, with plants like

Cakile maritima, Eryngium maritimum, Glaucium luteum, &c., the effect of drying is very small.

NOTE 11 (page 25)

The Effect of Sea-water Immersion on the Germinating Capacity of Seeds and Seed-vessels

Berkeley, Darwin, Martins, and others, long ago established the capacity of seeds to germinate after prolonged immersion in sea-water. The reader will find a *resumé* of their results in the appendix to Mr Hemsley's volume on the *Botany of the Challenger Expedition.* The subject is well illustrated in the original papers of those authors, and in my later papers on the flora of Keeling Atoll, and on the seed-drift of the Thames.

I may here remark that the earlier observers often pay more attention to the retention of the germinating capacity after sea-water immersion than to the degree of buoyancy. For this reason I have not been able to make great use of the buoyancy results of Martins, since he frequently does not distinguish between temporary and long-sustained buoyancy, an objection also pointed out by Thuret and Hemsley.

NOTE 12 (page 27)

The Buoyancy of the Fruits of Galium aparine

Norman and Sernander (see p. 172) attribute considerable buoyancy to these fruits on account of the hollow cavity in each. I used to find them in England in floating river-drift in autumn; and Norman observed them on the Scandinavian beaches. They do not, however, float long, as the cavity is open; and in two sets of my experiments they sank within a few days.

NOTE 13 (page 29)

The Buoyancy of the Seeds of Convolvulus sepium

This plant seeded freely in 1893 in the Lower Thames Valley, as at Molesey. I kept some of the seeds afloat for thirty-three months, of which the first nine months were spent in sea-water and the rest in fresh-water. One seed, at the end of the period, germinated healthily in the fresh-water.

NOTE 14 (page 26)

Other Long Flotation Experiments

Whilst keeping my collections of Thames sea-drift in water from year to year, I obtained a number of records of long "flotations." Thus in

several cases, as with Bidens cernua and different species of Carex, germination of the floating fruit took place in the water after a period of two years. The same is also true of the seeds of Iris pseudacorus and of the drupes of Sparganium ramosum. The last-named remained afloat in the vessels, with the seed still sound, after four years; and the fruits of Carex paludosa germinated afloat after three years in water. Many drift fruits and seeds did not germinate freely in the vessels until the second spring, that is, after a lapse of eighteen months; and in those cases where the experiments were still further prolonged, a few germinated in the vessels in the third and sometimes even in the fourth year.

NOTE 15 (pages 33, 280)

The Occurrence Inland of Silene maritima

Prof. Schimper appeared to be in doubt as to the inclusion of this littoral plant amongst those found in elevated mountain districts. However, an interesting note on the occurrence of this plant on the summit of one of the inland Norwegian mountains is given by Sernander (p. 405), and is referred to by me on page 280 of this work.

NOTE 16 (page 34)

The Buoyancy of the Seeds or Fruits of the British Beach-plants that also occur Inland

My experiments in the case of Armeria vulgaris, Artemisia, Cochlearia officinalis, Plantago, the maritime forms of Spergularia rubra with and without winged seeds, and Silene maritima disclose little or no floating capacity even after prolonged drying. Thuret obtained similar results for the Spergularia. It is unlikely that other plants of the group possess any floating power worth speaking of. As indicated in Note 71, the fruits of Raphanus maritimus float only for 7 to 10 days.

Nature disperses the fruits of Armeria vulgaris inclosed in the persistent calyx; but in this condition they float only for 2 to 4 days in sea-water, and the buoyancy of the capsule and seed is still more limited. They are sufficiently light to be blown some distance by strong winds, and the stiff hairs would cause them to adhere to a bird's plumage in the case of gulls nesting where the plants grow.

Reference to Matricaria inodora is made under Note 18.

NOTE 17 (page 35)

The Buoyancy of the Seeds or Fruits of the Group of British Littoral Plants that frequent Salt Marshes and Muddy Shores

Aster tripolium. The achenes, with or without the pappus, sink in fresh and salt water in a day or two even after a year's drying.

Glaux maritima
Plantago maritima
Samolus valerandi
Suæda fruticosa
Suæda maritima

The small seeds, or the seed-like nucules as in Suæda, have but little floating power even after prolonged drying.

Salicornia herbacea. Would be dispersed probably by floating portions of the plant, which, however, soon break down and the liberated seeds sink. The floating seedling thrives in sea-water and could be carried great distances (see Note 19).

Salsola kali. I experimented on this plant, both on the coast of Devonshire and in Chile, with the same results in both localities whether in the fresh state or after drying for weeks. The fruit sinks, but when the plant dries the fruit is often detached inclosed in the perianth, and floats in that condition in sea-water for a few days. Portions of the plant of various sizes bearing mature fruits all sank within ten days. It would seem at first sight, from the observations of Prof. Martins, that the fruits float for several weeks; but his experiments were mainly directed to testing the powers of germination after sea-water *immersion*; and it is often not at all clear whether *flotation* is implied or even to be correctly inferred. There is a slight suspicion of germination on the plant. Sea-birds doubtless aid in the dispersion of this plant; the dry crisp portions of the plant carrying fruits catch readily in one's clothes on account of the prickly-pointed leaves.

Scirpus maritimus. The fresh fruits float a few weeks in sea-water in most cases, but 10 per cent. remain afloat after two months. After drying for some months 30 per cent. remain floating after two months' immersion.

Triglochin maritimum
Triglochin palustre

The fruits float a few days or a week. Drying somewhat increases the buoyancy. Sir W. Buller in New Zealand found in the gullet of Anas superciliosa, the Grey Duck, numbers of the fruits of Triglochin triandrum.

NOTE 18 (page 35)

The Buoyancy of the Seeds or Fruits of the British Littoral Plants that are confined to the Beach

Arenaria (Honckeneya) peploides. The seeds float for many months in sea-water unharmed, 75 per cent. floating after a year. They never germinate in sea-water; but on being transferred to fresh water after many months in sea-water they germinate healthily in a few days. These seeds only float a few days in fresh water, all sinking within 10 days, and even after a year's drying they sink in a week or two. Precisely the same

results were produced in my experiments in 1892 on Cornish seeds, and in 1904 on Devonshire seeds. In the great contrast between their floating capacity in sea-water and in fresh water the seeds of this plant defy the general rule that seeds that float a long time in sea-water float also a long time in fresh-water. According also to Sernander the seeds float a long time in the sea. He says that the capsules float, but since they ultimately dehisce this could scarcely be efficacious in dispersal. Floating portions of the plant also aid in its dispersal, according to the same authority (p. 174). The plant forms great extended masses on the pebbly shores of Spitzbergen (Ekstam, p. 28).

Beta maritima. Thuret found that the dried fruits of this plant floated only two or three days in sea-water; whilst in my sea-water experiments the freshly gathered fruits floated only one or two days. Sernander speaks of them as fitted for dispersal from shore to shore; but this could only be to a limited extent. Martins and Thuret established by experiment the capacity of the germination of seeds of other species of Beta after long immersion in sea-water; and the first seems to imply that those of Beta vulgaris float for many weeks; but I am inclined to think an error lies here.

Cakile maritima. The fruits, even after long drying, float, as a rule, only a week and sink within ten days, the same results being afforded in my sea-water experiments in 1893 on fruits from Cornwall, and in 1904 on fruits from Devonshire. The fruits are common in the stranded drift on the north coast of Devonshire and may often be seen germinating there. They are also frequent in the beach drift of the Scandinavian coasts (Sernander, p. 156).

Crambe maritima. The fruits were kept floating by Sernander more than 13 days (p. 165). Martins implies that they floated for 45 days. Darwin says that they germinated after 37 days' immersion in sea-water, but does not specify that they floated all the time.

Crithmum maritimum. The ripe fruits readily separate into the two carpels, which are very buoyant and float in sea-water for months. In my experiments, 95 per cent. remained afloat after 10 months. It is remarkable that whilst in sea-water the spongy covering of the carpels retains its vitality, in fresh-water it becomes sickly and decays and the carpels lose their floating power, so that they float weeks instead of months as in the sea-water. The carpels are extremely light, being washed up in the spray and blown up by the wind amongst the lightest of the stranded drift of the Devonshire beaches. In a moderate gale they are often blown off the beach and up the cliff-faces.

Convolvulus soldanella. From 40 to 50 per cent. of the seeds float after six months in sea-water, and about 30 per cent. float after eighteen months, retaining up to the end their germinating capacity. Sernander implies that the plant is not found on the Scandinavian coast to the north of Nissum Fjord in Denmark. It is known, however, to occur in the south

of Scotland. (I am indebted to Mr. Millett for his extremely kind assistance in experimenting on this plant about ten years since.)

Eryngium maritimum. The fruits float in sea-water, as a rule, only 3 or 4 days and all sink within a week. After drying for three months, the floating period is only increased by a day or two. Though not at all suited for transport for any distance by the currents, the carpels, on account of their long prickly calyx teeth, would readily become entangled in a bird's plumage, and doubtless they are dispersed usually in that fashion.

Euphorbia paralias. The seeds float a long time unharmed in the sea. In my experiments at least 90 per cent. remained afloat after six weeks in sea-water. On account of their small size they are liable to be overlooked in beach drift; but they are to be found stranded on the sands of our southern coasts, and they came under my notice in abundance in the seed-drift of the Sicilian beaches.

Glaucium luteum.—The seeds have no proper buoyancy even after prolonged drying. On account of their oiliness they will float at first on still water; but they can be made to sink at once or in a day by dropping water upon them. The mode of dispersal is problematical.

Lathyrus maritimus.—The seeds are evidently able to float a long time. They were, according to Sernander (p. 178), found in quantities by J. Schmidt cast up on some sand-islets near Falster in Denmark; and the plant is regarded by Norman as distributed over the coasts of Arctic Norway through the agency of the currents. They have, as observed by Schmidt, considerable floating powers. Some small leguminous seeds, seemingly of this species, which I found in the beach drift of Woollacombe Sands, Devonshire, floated uninjured for many weeks in sea-water.

Matricaria maritima, maritime variety of M. inodora. The fruits floated in my experiments unharmed after eight months in sea-water. In an experiment made some years since on the fruits of the inland form I noted that they had little or no buoyancy; but it is necessary to repeat the observation. Sernander (p. 181) supports Norman's view that these plants are spread by the currents in Arctic Norway. The fruits occur in the Baltic sea-drift and also in fresh-water drift. M. inodora is found on sandy beaches in Nova Zembla. I am inclined to regard the maritime form from the dispersal standpoint as a distinct species.

Polygonum maritimum.—I have made observations on this plant in Devonshire, the Lipari Islands, and the coast of Chile. As in the case of several other species of Polygonum tested by me the fruits have little or no buoyancy, but inclosed in the perianth they float three or four days. The entire plant floats; but portions placed in sea-water sank within five or six days. Shore-birds can alone explain the wide distribution of this species.

The structural characters of some of these fruits or seeds are in their relation to buoyancy discussed on page 115. It may be here observed that the valuable results obtained by Prof. Martins in testing the germinating

capacity of the fruits and seeds of several of the shore-plants above mentioned, after long immersion in sea-water, are at times not to be depended on for the flotation indications, the persistence of the seed's vitality being the special purpose of his research. His negative results as regards germination are not, however, always conclusive, since the period employed from April to June was quite insufficient. In many of my experiments seeds after long flotation in sea-water did not germinate for a year or more afterwards. If his investigation had been extended, the opinion that the Ranunculaceæ, the Malvaceæ, and the Convolvulaceæ are apparently least able to resist the action of sea-water would never have been formed. A very large amount of evidence now shows that most seeds or fruits that are at all well protected will germinate after long immersion in sea-water. But all experiments must be well safeguarded and extended over a year or two. The necessity of this was long since shown by Thuret. By employing double sets of seeds he ascertained that in a third of the species germination failed not only in the case of the seeds immersed in sea-water, but also in those that had not been placed in sea-water at all. Future investigators may, however, regard the buoyant qualities of seeds or fruits with their associated structural characters as offering now the true line of research. Observers beginning with Berkeley and Darwin down to the present time have quite established the fact that seeds as a rule germinate freely after long sea-water immersion.

NOTE 19 (page 35)

On Germination in Sea-water

During my experiments on the buoyancy of about 270 British plants, about a fourth of them (including most of those with buoyant seeds or fruits) were subjected to prolonged immersion in sea-water from periods varying from six to thirty-three months. If we except plants like Aster tripolium, Salicornia herbacea, Triglochin maritimum, &c., that live normally in salt marshes, or on the muddy banks of estuaries, only one of the whole number, namely, Ranunculus sceleratus, displayed the capacity of germination in sea-water. Amongst the plants that failed may be mentioned the following that are confined to the sea-beach—Arenaria peploides, Cakile maritima, Convolvulus soldanella, Eryngium maritimum, Euphorbia paralias, Glaucium luteum, and we may here include Crithmum maritimum of the rocky coasts. Of the beach-plants that also grow inland, Silene maritima and Spergularia rubra (excepting the form found on muddy coast flats) likewise failed. Amongst the plants of miscellaneous inland stations that failed were Atriplex patula, Bidens cernua, B. tripartita, Calla palustris, several species of Carex both from dry and wet situations, Convolvulus arvensis, C. sepium, Hydrocotyle vulgaris, Iris pseudacorus,

several species of Juncus, Lycopus europæus, Mentha aquatica, Ranunculus repens, Rhinanthus crista galli, several species of Rumex, Scutellaria galericulata, Sparganium ramosum, &c.

In nearly all the plants that failed to germinate in sea-water the capacity of readily germinating in fresh water was displayed. The restraining power of immersion in sea-water was illustrated over and over again in my experiments. During the course of an experiment seeds removed from the sea-water vessel and placed directly in a vessel of fresh water kept beside the other germinated in a few days, whilst those left in the sea-water never germinated, though often kept there for months after. It was also noticeable that a previous sea-water immersion favoured early germination in fresh water. It may be added that most of the experiments were on floating seeds and seed-vessels, though germination also occurred in the sunken state.

It was ascertained in the exceptional case of Ranunculus sceleratus, that although germination took place in sea-water, it was only after a prolonged soaking of months had prepared the way. Of a number of its seed-like fruits placed in fresh water and in sea-water in April and kept under the same conditions, those in fresh water germinated freely in a week or two, whilst those in sea-water did not begin to germinate until the following October. Whilst the floating seedlings produced by germination in fresh water grew vigorously and developed roots, those resulting from germination in sea-water and left in the vessel only attained a length of four millimetres in two months, developed no roots, and showed only the first leaf. The sea-water seedlings were pale green, and in their stout fleshy appearance contrasted greatly with the slender fresh-water seedlings,

With regard to the germination in sea-water of the plants of the salt marsh and of the mud-flats of estuaries, the following observations may be made. With Aster tripolium the seeds germinate readily in sea-water even when its density is raised by evaporation to 1·040; and I think that by a carefully graduated series of experiments they could be induced to germinate in brine. The seeds of Salicornia herbacea germinate in sea-water more readily than in fresh water; and the sea-water seedling is much the more vigorous and healthy of the two. I kept the floating seedlings in sea-water for about ten weeks from the date of germination, when they had developed the second joint and were throwing out rootlets. After that, unless placed in salt-mud, they became sickly and died. The floating seedling can evidently disperse the species. I found with Spergularia marina, the maritime form of S. rubra, that seeds of the plants growing on a sandy beach did not germinate in sea-water, only those from plants growing on muddy coast-flats doing so. But the sea-water seedlings, unlike those of Salicornia herbacea, but like those of Ranunculus sceleratus, when left in sea-water did not thrive. The seeds of Triglochin maritimum, as well as those of T. palustre, behave very similarly in sea-water, germinating readily, the liberated seedlings thriving afloat and producing the plumule.

The ultimate test of the capacity for germinating in sea-water seems to lie in the behaviour of the seedling when left in the sea-water. Unless it belongs to a characteristic plant of the salt marsh or of the estuary, like Salicornia, it makes but little attempt at growth whilst afloat in sea-water, showing no rootlets, though at times developing the plumule.

The germination of seeds in sea-water also attracted the notice of Darwin; but his results in some respects are scarcely those I should have looked for (*Gardener's Chronicle*, May, 1855, and *Journ. Linn. Soc.*, vol. i., p. 130, 1857). Out of the seeds of 87 plants placed in sea-water to test their capacity of germination when afterwards planted, in three cases, those of Tussilago farfara, Convolvulus tricolor, and the garden Orache (Atriplex), the seeds germinated under the water, the freed seedlings, as with the two first named plants, living in the sea-water for some time after. Darwin was evidently himself surprised at these results, and I am quite unable to understand them. In England and in the tropics I have carried on prolonged sea-water experiments on the seeds of at least fifteen species of Convolvulus and Ipomea (including the beach plants C. soldanella and I. pes capræ) and have never obtained such a result. The seeds will nearly always germinate well in fresh water; but in sea-water the process begins, as indicated by the swollen seed, and then aborts, the embryo dying (see page 83). The seeds of Atriplex patula, though a long time in sea-water in my experiments, made no attempt to germinate there. Neither Prof. Martins, who experimented upon the effects of sea-water immersion on the seeds of nearly 100 plants, including many coast species, nor M. Thuret, who experimented in sea-water on the seeds of 251 plants, the experiments being in some cases prolonged for more than a year, make any reference, as far as I could gather from their writings, to any cases of germination in sea-water. Darwin's results, however, are always significant in matters of dispersal; and perhaps one of my readers will be able to experiment again on his three plants.

When in Hawaii, I made some observations on the germination of Batis maritima in sea-water, a plan with which I was also familiar in its home in the salt-water pools of the coast of Peru. The mature fruits, on being freed from the parent plant in sea-water, float away, and in from one to two weeks they break down from decay, setting free the seeds. The seeds float in sea-water indefinitely, their buoyancy only terminating with their germination, the first seeds germinating afloat about six weeks after the breaking down of the fruit, whilst the rest continue to float in the sea-water during the next three months, some of them germinating at intervals, and all of them doing so eventually. Strange to say, although the seedlings remained healthy whilst afloat in the sea-water, they made no effort either to separate the cotyledons or to produce a plumule.

NOTE 20 (page 42).

On the Maximum Heights reached by some Shore Plants in their Extension Inland in Vanua Levu, Fiji

Since they occupy the "talasinga" districts described in the following note, these shore plants would be expected to extend as high as those districts extend, namely, to about 1,500 feet above the sea. This indeed represents their limit excepting in one instance; but many fall considerably short of this elevation.

Canavalia obtusifolia, variety, 700 feet, rare.

Cassytha filiformis, 950 feet.

Cerbera Odollam, 1,200 feet: 2,600 feet in one exceptional case on the slopes of Mbatini.

Colubrina asiatica, 400 feet.

Cycas circinalis, 1,100 feet.

Derris uliginosa, 1,000 feet, rare.

Ipomea pes capræ, 1,300 feet.

Morinda citrifolia, 700 feet.

Scævola Kœnigii, not common inland, and rarely over 100 feet above the sea; but it may occur miles from the beach, as near Vatu Levoni, where a few stunted plants were growing five miles from the coast.

Vitex trifolia, 1,300 feet, usually more or less unifoliolate and procumbent.

Unless otherwise stated all the plants above named are common inland, as also are *Premna tahitensis*, *Tacca pinnatifida*, *Tephrosia piscatoria*, *Hibiscus tiliaceus*, &c.; but I have made no note of *Thespesia populnea* occurring far off the beach.

NOTE 21 (pages 42, 43)

On the Dwarfing of Shore Plants when extending Inland into the "Talasinga" Plains in Vanua Levu.

Premna tahitensis, 9 or 10 feet high at the coast, may here be only 3 feet high. Other trees like *Morinda citrifolia* become also stunted. *Cerbera Odollam*, a moderate-sized tree at the coast, may in the "talasinga" plains be only 4 to 6 feet high, but it here displays distinct varietal characters. Whilst the shore trees of Cerbera Odollam have broad leaves (length 3 times the breadth) with obtuse points, and short, stout flower-peduncles ($1\frac{1}{2}$–2 inches), the inland or "talasinga" species has long lanceolate leaves (length 7 or 8 times the breadth), and long, slender flower peduncles (3 inches). However, intermediate forms are common, the broad-leaved coast tree approaching the inland plant and *vice versâ*.

NOTE 22 (page 43)

THE "TALASINGA" PLAINS OF VANUA LEVU, FIJI

Amongst the most conspicuous features of the north and north-west or lee sides of the large islands of Vanua Levu and Viti Levu are the extensive rolling plains that extend from the sea-border for some miles inland to the foot of the mountains. It is to those of the first-named island that the following remarks strictly apply; but no doubt they will serve equally well for those of the other island. In the first volume on the geology of Vanua Levu, reference is frequently made to this subject, and the reader may profitably look at the remarks there made.

Here the mountain-forests more or less abruptly cease, and we have an undulating region of grass, reeds, and ferns dotted over with Casuarinas, Pandanus trees, Cycads, Acacias, and shrubby growths. Though the list of plants characteristic of these plains is not small, they are not, as a rule, numerous in any one locality, and the general appearance is one of aridity. A dry, crumbling soil, often deeply stained by iron-oxide, is plentifully exposed; and blocks of basic volcanic rocks in all stages of disintegration are strewn over the surface in many localities. Rivers, fed by the heavy rainfall of the forested slopes of the mountains, traverse these regions, but, as a rule, receive no tributaries; and the districts have, in fact, well earned the name given to them by the natives of the "talasinga," or sun-burnt, lands.

The vegetation, though sparse and scanty in comparison with that of the forests, is sufficiently varied when it comes to be more closely examined. In one locality we may have extensive tracts covered with Gleichenia, Pteris, and other ferns of the bracken habit. In another, tall reeds (Eulalia) and grasses cover large areas. Here, more than one species of Tacca (T. pinnatifida and T. maculata) thrive. There, the Turmeric (Curcuma longa) abounds. Trailing over the soil in one place we notice Ipomea pes capræ, in another the Yaka (Pachyrrhizus trilobus), and in another the procumbent unifoliolate form of Vitex trifolia. Amongst the shrubs and small trees we observe in different localities the Sama (Commersonia echinata), the Mbulei (Alstonia plumosa—one of the rubber plants), Mussænda frondosa, Melastoma denticulatum, and Nelitris vitiensis, the Nunga-nunga. Dodonæa viscosa, found in similar regions in Australia and New Zealand, abounds in places; and here and there may be seen species of Hibbertia, another Australian genus. Fagræa Berteriana, the Mbua tree, grows abundantly in certain districts, as in the Mbua plains, and Gardenias are at times abundant. One or two characteristic beach-plants have been already mentioned, and amongst others particularly frequent in these plains are Cassytha filiformis, Cerbera Odollam, Morinda citrifolia, and Premna tahitensis.

When these talasinga districts approach the forests, patches of wood

occur at intervals, and we observe here the Candle-nut Tree (Aleurites moluccana), the Vunga (Metrosideros polymorpha), and the Thau-kuro (Casuarina nodiflora). Such are some of the botanical features of these districts; but the reader will acquire a sufficiently correct general notion of the floral physiognomy of these regions if he bears in mind their most conspicuous characters, those of an undulating region more or less covered with ferns, tall reeds, and grass, and dotted over, either separately or in clumps, with Casuarinas (C. equisetifolia), Screw-pines (Pandanus odoratissimus), Cycads (C. circinalis), and Acacias (A. Richii, &c.).

However, the peculiar vegetation of these plains often ascends the lower slopes of the mountains, reaching to various elevations. In Vanua Levu it often ceases at 900 or 1,000 feet, but it may only reach to 400 or 500 feet, and, on the other hand, not uncommonly it ascends to as much as 1,500 feet, the greatest elevation recorded by me being 1,600–1,700 feet in the Sealevu district. It extends miles inland, and where conditions are suitable it may reach the heart of the island.

Different explanations have been offered of the origin of the peculiar vegetation of the leeward slopes of these islands. It is, however, a phenomenon that is presented over much of the globe by islands lying in the track of regular winds, the weather, or wet, side being densely wooded, whilst the lee, or dry, side is covered with grass, ferns, and similar vegetation. The predisposing cause must be climatic; and although Mr. Horne's explanation attributing it to the effect of fires and to a faulty system of native cultivation (pp. 80, 132) may be doubtless true in certain localities, the influences at work here must be the same as are at work in other islands and on continental coasts in other parts of the world.

But for all that it is not easy to give a definite explanation even from a meteorological standpoint. Those who are interested in this subject will recall the desert districts of Australia and the dreary sandy wastes of the coast of Northern Chile and Peru; and they will be cautious in venturing on a definite explanation even with such relatively unimportant examples of the same principle as are exhibited by the islands of Fiji. Dr. Seemann, writing of these "talasinga" plains (p. xii), remarks that "their very aspect is proof that rain falls in only limited quantity," the mountainous backbone of the islands intercepting, as he holds, much of the rainfall. But the subsequent observations of Mr. Holmes, at Delanasau, in the "talasinga" district on the north-west side of Vanua Levu, have shown that there is by no means a small rainfall in this locality, the average rainfall, for instance, for the seven years ending December, 1877, being 113 inches, which must be quite two-thirds or three-fourths of the fall on the weather side of the island (see p. 215); whilst the average number of days on which rain fell was 156. The true cause would seem to lie in the excessive dryness of the air on the lee side of the islands between the rains, and the whole matter may, perhaps, be one rather for the hygrometer than for the rain-gauge. I have no comparative data bearing on this

point; but Mr. Holmes, whose observations as here quoted are from Horne's *Year in Fiji*, found that the mean relative humidity for 1875 at 1 P.M. was 63, which is certainly very low for the tropics. I may remark that, as far as personal experience goes, the climate on the lee side of Vanua Levu is much more enervating, much less healthy, and the air is far more "drying" than on the side exposed to the trade-wind.

Geological characters, as I found, explained nothing in this connection, the "talasinga" vegetation sometimes occurring on basaltic areas, at other times on the "soapstone" or calcareous mud-stone, and again on coarser tufaceous rocks. In my volume on the geology of Vanua Levu (p. 57), it is pointed out that the extensive disintegration of the basaltic rocks, that are exposed on these plains in places, affords evidence of the great antiquity of these "talasinga" districts in their present unforested condition. The extent to which these rocks have weathered downward is remarkable. In some places they are decomposed to a depth of ten feet and more. The same inference is to be drawn from the occurrence of fragments of limonite, or bog-iron ore, over these plains, marking as they do original swampy tracts that, with a few exceptions, have long since disappeared. Such deposits indicate that these plains have been for ages in the same condition. . . . It may be added that, according to Mr. Lister and Mr. Crosby, the features of the "talasinga" plains occur in the Tongan Group on the leeward sides of the islands of Eua and Vavau.

NOTE 23 (page 43)

Schimper's Grouping of the Indo-Malayan Strand-flora

It is divided into four formations—the Mangrove, the Nipa, the Barringtonia, and the Pes-capræ. The two last make up my Beach-formation, the Barringtonia formation comprising the trees, shrubs, &c., immediately lining the beach, and the Pes capræ including the creepers and bushes of the beach itself. In the Pacific islands it is not always easy to preserve this distinction. The Nipa formation corresponds in some respects with my Intermediate or Transition formation, lying as it does between the mangrove-belts and the woods of the interior; but the swamp-palm (Nipa fruticans) that forms it in the mass is not found in Fiji or, indeed, in the Pacific islands, excepting the Solomon and Caroline Groups.

NOTE 24 (page 44)

Grouping of some of the Characteristic Plants of the Strand-flora of Fiji

(a) *Beach-formation.*—Calophyllum inophyllum, Thespesia populnea, Triumfetta procumbens, Carapa moluccensis, Canavalia obtusifolia, Vigna

lutea, Pongamia glabra, Sophora tomentosa, Cæsalpinia Bonducella, Acacia laurifolia, Barringtonia speciosa, Terminalia Katappa, Gyrocarpus Jacquini, Pemphis acidula, Morinda citrifolia, Guettarda speciosa, Wedelia biflora, Scævola Kœnigii, Cordia subcordata, Tournefortia argentea, Ipomea pes capræ, Cassytha filiformis, Hernandia peltata, Pandanus odoratissimus, &c.

(b) *Mangrove-formation.*—Carapa obovata, Rhizophora mucronata, Rhizophora mangle, Bruguiera Rheedii, Lumnitzera coccinea, Scirpodendron costatum, &c. (See below.)

(c) *Intermediate or Transition-formation.*—Hibiscus tiliaceus, Heritiera littoralis, Smythea pacifica, Derris uliginosa, Entada scandens, Barringtonia racemosa, Cerbera Odollam, Clerodendron inerme, Vitex trifolia, Excæcaria Agallocha, &c.

N.B.—It is not possible to draw a definite line between the plants of the mangrove swamp and those of the tracts around. Several of the plants placed in the intermediate formation, such as Heritiera littoralis, Entada scandens, Excæcaria Agallocha, &c., are just as much at home amongst the mangroves. In the same way it is often difficult to distinguish between the Beach and the Intermediate formations, and plants like Cerbera Odollam, Hibiscus tiliaceus, and Vitex trifolia belong equally to both.

NOTE 25 (page 47)

The Strand-flora of the Tahitian Region

Drake del Castillo's *Flore de la Polynésie française* deals mainly with the Society or Tahitian Islands, but also with the Marquesas, Paumotus, Gambier Islands, and Wallis Island. The last-named, however, lies in Western Polynesia, and is not dealt with in this connection. There is no reason to believe, judging from the general character of the islands and from Cheeseman's memoir on the Rarotongan flora, that the strand-plants of the islands of the Cook and Austral Groups, which also belong to this region, differ materially from those of the Tahitian islands proper. Rarotonga, however, possesses Entada scandens, not recorded as a growing plant from any other part of East Polynesia, excepting perhaps Mangaia in the same group.

NOTE 26 (page 48)

The Fijian Shore-plants not found in Tahiti

Although most of these plants, such as Barringtonia racemosa, Clerodendron inerme, Entada scandens, Excæcaria Agallocha, Heritiera littoralis, Smythea pacifica, &c., have fruits that float for months, and could have reached Tahiti as readily as some of the beach-plants that have successfully established themselves, there are a few like Dalbergia monosperma

Derris uliginosa, and Scirpodendron costatum, the fruits of which only float for weeks, and it is possible that they may have been unable to reach there.

NOTE 27 (page 49)

THE INTRUDERS INTO THE BEACH-FLORA FROM THE INLAND PLANTS OF TAHITI

Drake del Castillo mentions several, such as species of Boerhaavia, that could only be occasional intruders; but it is noteworthy that Gardenia tahitensis appears to be a genuine recruit from inland. The xerophilous habit of the Pacific Gardenias and their station, usually near the coast, however, would render this possible.

NOTE 28 (page 52)

THE LITTORAL PLANTS OF THE HAWAIIAN ISLANDS

Species.*	Origin.			Distribution.			Characters of fruit or seed.				
		Introduced					Size.†		Buoyancy.		
	Indigenous.	By aborigines in ancient times.	By Europeans soon after discovery.	Old World.	New World.	Both Worlds.	Large.	Small.	Float for months.	Sink at once or in a few days.	Attract frugivorous birds.
Acacia Farnesiana	...	...	+	...	...	+	...	+	weeks	...	?
Cæsalpinia Bonducella	+	...	...	...	...	+	...	+	...	+	...
Calophyllum inophyllum	...	+	...	+	...	...	+	...	+	...	...
Cassytha filiformis	+	...	...	...	...	+	...	+	+	...	+
Colubrina asiatica	+	...	...	+	...	...	...	+	+	...	...
Cordia subcordata	...	+	...	+	...	...	...	+	+	...	...
E Cuscuta sandwichiana	+	...	...	...	...	...	...	+	...	+	...
Cocos nucifera	...	+	...	...	...	+	+	...	+	...	...
P Gossypium tomentosum	+	...	...	...	...	...	...	+	...	+	...
P Heliotropium anomalum	+	...	...	...	...	...	...	+	...	+	...
Heliotropium curassavicum	+	...	...	...	...	+	...	+	...	+	...
Herpestis Monnieria	+	...	...	...	...	+	...	+	...	+	...
Hibiscus tiliaceus	...	+	...	...	...	+	...	+	+	...	...
Ipomea glaberrima	+	...	...	+	...	...	...	+	+	...	...
Ipomea pes capræ	+	...	...	...	...	+	...	+	+	...	...
E Jacquemontia sandwicensis	+	...	...	...	...	...	...	+	...	+	...
E Lipochæta integrifolia	+	...	...	...	...	...	...	+	...	+	...
Morinda citrifolia	...	+	...	+	...	...	...	+	+	...	?
Mucuna gigantea	+	...	...	+	...	...	+	...	+	...	...
Pandanus odoratissimus	...	+	...	+	..	...	+	...	+	...	...
Portulaca oleracea	...	+	...	...	...	+	...	+	...	+	...
Scævola Kœnigii	+	...	...	+	...	...	...	+	+	...	+
Sesuvium Portulacastrum	+	...	...	...	...	+	...	+	...	+	...
Tacca pinnatifida	...	+	...	+	...	...	...	+	+	...	...
Tephrosia piscatoria	+	...	...	+	...	...	...	+	...	+	...
Terminalia Katappa	...	...	+	+	...	...	+	...	+	...	...
Thespesia populnea	...	+	...	+	...	...	...	+	+	...	...
Tribulus cistoides	+	...	...	...	+	...	...	+	...	+	...
Vigna lutea	+	...	...	...	...	+	...	+	+	...	...
Vitex trifolia	+	...	...	+	...	...	...	+	+	...	+

* There are three endemic species here included which are preceded by E. Two species preceded by P are confined to Polynesia. Most of the plants are at present typically littoral, though often also occurring inland.

† All fruits or seeds, an inch or over in size, that could not have been transported to Hawaii by birds are regarded as large.

NOTE 29 (page 54)

Botanical Notes on the Coast-plants of the Hawaiian Islands

[The following remarks have been extracted from my journals and represent some of the field-notes of journeys made in the more interesting localities.]

(1) *Walk along the Puna Coast, Hawaii, from Punaluu to Hilo* (Dec. 26, 1896, to Jan. 6, 1897).—For the first two to three miles to Kamehame Point, the following plants were noticed on the flows of smooth ropy lava that formed the cliff-bound coast—Capparis sandwichiana, Jacquemontia sandwicensis, Ipomea insularis, Lipochæta lavarum, Portulaca villosa, Tephrosia piscatoria, Tribulus cistoides, Waltheria americana, &c. Beyond this point Scævola Kœnigii was abundant in places on the old lava-flows near the sea, and further on patches of Myoporum sandwicense growing, not as a tree 20 to 30 feet high, as in the mountains, but as a prostrate shrub with fleshy leaves. Vegetation similar to that above described occurred on the surface of the old lava-flows that constituted the cliff-bound sea-border as far as Kapapala Bay. On the sandy beach at Kapapala Bay grew Ipomea pes capræ, serving as host to Cuscuta sandwichiana. In the vicinity of the house at Keauhou there were a few Coco palms and Pandanus trees, whilst Capparis sandwichiana and Morinda citrifolia were growing on the adjacent lava-fields.

Morinda citrifolia and Tephrosia piscatoria grew on the lava flows between Keauhou and Apua. On the beach at Apua, Ipomea pes capræ and Scævola Kœnigii were abundant, the last extending a few hundred yards inland on the lava. Further east the inland bush, made up of Cyathodes tameiameiæ, Metrosideros polymorpha, &c., descended to the coast to within a few hundred yards of the sea. In crossing the lava coast plains to Kapa-ahu I observed Morinda citrifolia growing frequently out of the cracks in the bare lava-rock, and an occasional solitary tree of Erythrina monosperma growing also from the fissures.

Before reaching Kapa-ahu we passed the site of an old coast village, named Laepuki, where there were growing from forty to fifty Coco-nut palms, as well as another village, represented by a solitary house, and named Kamomoa, where there were 27 Coco-nut palms and a few Pandanus trees. Kapa-ahu, with its numerous Coco-nut palms, was more like a South Sea coast village than any before seen; and the coast vegetation suddenly acquired a South Pacific character.

At Pulama, for instance, about a mile west of Kapa-ahu, where the ancient lava-flows, fairly vegetated, terminate at the sea in cliffs 20 or 25 feet high, there is a curious and quite unexpected development of a littoral flora such as we should see in the South Pacific. Here, growing on the broken lava surface at the brink of the cliffs and overlooking the sea, thrive Cæsalpinia Bonducella, Cocos nucifera, Ipomea pes capræ,

Ipomea glaberrima, Morinda citrifolia, Pandanus odoratissimus, Scævola Kœnigii, Sesuvium Portulacastrum, Thespesia populnea, and Vigna lutea. This shore-belt of characteristic littoral plants is backed by vegetation more inland in its character, amongst which Aleurites moluccana, Dodonæa viscosa, Erythrina monosperma, Ipomea insularis, I. bona nox, Osteomeles anthyllidifolia, &c., are to be observed. Such a shore-belt of typical littoral plants is rarely to be found in the large island of Hawaii; and its usual position at the margin of cliffs, and raised 20 or 25 feet above the sea, is rather suggestive of an uplift in recent times of this part of the coast.

Between Kapa-ahu and Kalapana is a low country occupied mostly by Guavas, and often turfy. At Kalapana, which is a large village situated on a grassy plain by the sea, Coco palms and Pandanus trees abound, and Mucuna gigantea and Cæsalpinia Bonducella are frequent near the coast, whilst Ipomea pes capræ is common on the beach. Calophyllum inophyllum is planted near the houses. Here Osteomeles anthyllidifolia in its dwarfed form descends to the edge of the cliffs. About half a mile beyond Kalapana is the hamlet of Kaimu, and here among the Coco palms close to the beach I noticed four Loulu palms (Pritchardia Gaudichaudii). Beyond Kaimu the trees and shrubs of the inland wood, Metrosideros polymorpha, Cyathodes tameiameiæ, &c., descend on the spurs of old lava-flows close to the coast; whilst Pandanus and Morinda citrifolia with Mucuna gigantea are common near the sea as far as Kehena, where there are plenty of Coco palms. I approached Opihikao through as fine a Pandanus forest as I have ever seen, the large Bird's Nest Fern (Asplenium nidus) growing half-way up their trunks, adding picturesqueness to the scene, whilst Mucuna gigantea was a common climber. Beyond Opihikao the inland woods descend to the coast. Thence on to Makuu the coasts are mostly occupied by Pandanus forests, and the lower coast road from Makuu to Hilo traverses a region where these Pandanus trees abound, extending far inland. Scævola Koenigii and Ipomea pes capræ are common on the coast near Coco-nut Island, Hilo Bay.

It may be added that the agency of the wild goat explains the dispersal of Myoporum sandwicense, Morinda citrifolia, Tephrosia piscatoria, Waltheria americana, &c., over the almost bare surfaces of the lava flows on the Puna coast. Goat droppings were frequent under the patches of Myoporum and Waltheria. In some of them I found the entire seeds of Portulaca oleracea and the small cocci of Euphorbia pilulifera, weeds common in the district.

(2) *Coasts of the Kalae Promontory and its Vicinity, Hawaii.*—This is the most southerly portion of the group, and it is on the eastern coasts of this district that many of the North American drift logs are embayed and stranded. At Kamilo, to the east of the promontory, there is a long beach of calcareous sand where Heliotropium anomalum, Scævola Kœnigii, and Tribulus cistoides grow in abundance, whilst Sesuvium Portulacastrum

thrives on the beach and in brackish pools. Portulaca lutea (Sol.), Ipomea glaberrima (Boj.), and Jacquemontia sandwicensis also occur. Where the beach-sand has encroached on the adjacent lava surface, the Scævola covers extensive tracts off the beach, and is stunted. I noticed a solitary thicket of Thespesia populnea on the beach.

The actual headland of Kalae is wind-swept and covered with grass, amongst which Portulaca villosa and Sida fallax thrive. By the sea occur Scævola Kœnigii and Ipomea pes capræ, and there is some Sesbania tomentosa near the point. Waiheiaukini beach is shut in between the lofty arid slopes of the promontory on one side and a modern lava-flow on the other side. Here Scævola Kœnigii grows in quantity, together with Ipomea pes capræ, Tribulus cistoides, Sida fallax, and Jacquemontia sandwicensis, whilst Cuscuta sandwichiana is abundant, finding its hosts in the first four plants just named.

(3) *South Kona Coast*, *Hawaii*.—The coast here, as exemplified by that between Kapua and Hoopuloa, is mostly bare lava. Here and there, a little coral sand collects amongst the lava blocks of the rubbly shore, and it is in such places that Scævola Kœnigii and Ipomea pes capræ find a home and apparently thrive, whilst Hibiscus tiliaceus and Morinda citrifolia grow behind. I observed Cordia subcordata and one or two specimens of Pritchardia Gaudichaudii by the coast on the south side of Milolii. Around a brackish pool at Kapua I observed Heliotropium curassavicum, and Acacia Farnesiana was to be seen growing on the beach at Okoe. On the lava coast between Hoopuloa and Papa, two miles to the north, Tephrosia piscatoria was very abundant.

(4) *North Kona Coast*, *Hawaii*.—I examined the coast between Kailua and Kiholo. White beaches are common south of Keahole Point, the coast further north being usually lava-bound with sandy beaches here and there. Heliotropium anomalum, Ipomea pes capræ, and Sesuvium Portulacastrum are the commonest beach plants on this coast. Scævola Kœnigii is also abundant in places, whilst Tribulus cistoides and Morinda citrifolia are also fairly common on the beaches. The Morinda also grows on the adjacent lava flats; but on both sand and rock it is evidently usually self-sown, since seedlings are to be seen near the older plants. Heliotropium curassavicum is to be seen here and there on the sand all along the coast, but nearly always associated with H. anomalum. Jacquemontia sandwicensis occurs occasionally on the beach; and Cuscuta sandwichiana is abundant in places, growing generally on Ipomea pes capræ, but sometimes on Scævola Kœnigii. Brackish water ponds are common on the coast inside the beaches, Ruppia maritima flourishing in the water, with Sesuvium Portulacastrum growing at the edges. Sometimes Hala trees (Pandanus odoratissimus) fringe the borders of the pools. I noticed Pritchardia Gaudichaudii on the coast at Kiholo, and I learned that Cordia subcordata was once common here as on other parts of the Kona coast; but it has died out as in most other localities.

(5) *Kohala Coast, Hawaii.*—Several littoral plants are scantily represented on the beach of black sand at the mouth of the Waimanu valley, especially Ipomea pes capræ, Morinda citrifolia, Pandanus odoratissimus, and Scævola Kœnigii. The Pandanus covers the adjacent precipitous slopes up to a height of several hundred feet above the sea. Ipomea pes capræ is abundant on the sand dunes backing the beach at Waipio. I observed Naias marina in the Waipio River just inside the mouth. No one seems to have recorded the plant from the group since Chamisso found it in Oahu.

(6) *Hamakua Coast, Hawaii.*—Not many opportunities presented themselves on this cliff-bound coast of finding littoral plants. At the mouth of a gulch between Ookala and Laupahoehoe I found growing at the coast Vitex trifolia (var. unifoliolata) in quantity, together with Morinda citrifolia, Scævola Kœnigii, and Pandanus odoratissimus, the last-named clothing the hill-slopes overlooking the sea.

(7) *The Coasts of Oahu.*—The littoral vegetation of the south-east portion of the island from Diamond Head round to Waimanalo is, as a rule, scanty. Ipomea pes capræ and Tribulus cistoides prevail to Koko Head, and on the rubbly coast between that headland and Makapuu Point occur Tephrosia piscatoria, different species of Lipochæta, &c. Between Makapuu Point and Waimanalo, Scævola Kœnigii and Vitex trifolia (var. unifoliolata) are fairly abundant, the former growing on the rocky slope at the base of the cliffs, and raised perhaps some 20 feet above the sea. Along the whole east coast of the island the littoral vegetation is rarely well represented. However, Ipomea pes capræ is common everywhere, whilst Scævola Kœnigii occurs frequently, and here and there a few plants of Morinda citrifolia are seen on the beach, while thickets of Hibiscus tiliaceus mark in some localities the mouths of streams.

On the north coast of Oahu, as on the Waialua and Waimea beaches, the one-leaved variety of Vitex trifolia is common, together with Ipomea pes capræ and Euphorbia cordata; whilst Acacia Farnesiana is frequent on the Waialua beach, its pods being much appreciated by the cattle. Occasionally, as by the bridge at Waimea, Colubrina asiatica and Thespesia populnea are to be noticed.

Shore vegetation is a little better represented on the beaches at and near Kaena Point, the north-west corner of the island. Here on the sand we find often in abundance Heliotropium anomalum, the same variety of Vitex trifolia, Scævola Kœnigii, and Ipomea pes capræ; whilst on the rocks bordering the beach occur Gossypium tomentosum, Jacquemontia sandwicensis, Tribulus cistoides, Vigna lutea, and more than one species of Lipochæta, the last being derivatives from the inland flora.

On the west coast of the island true shore-plants play an inconspicuous part. Ipomea pes capræ is common on the beaches, and such plants as Acacia Farnesiana, Jacquemontia sandwicensis, Gossypium tomentosum, and Tribulus cistoides immediately border the beach. Ipomea tuberculata

is a frequent intruder as well as the recently introduced Algaroba tree (Prosopis dulcis). Acacia Farnesiana also extends inland, covering entire large areas and forming in the Waianae valley extensive thickets impenetrable for the cattle. It occupies great districts near the coast in different parts of Oahu, and with Hibiscus tiliaceus is to be found far inland. The cattle are active dispersers of its seeds. (See Note 30.)

True beach plants are infrequent at the mouth of Pearl Harbour, although the coast is well suited for them. Here I found Heliotropium anomalum, H. curassavicum, Jacquemontia sandwicensis, Lipochæta integrifolia (a true beach plant), Herpestis Monnieria, &c. Batis maritima occurs in one or two localities around Oahu, but it is, according to Hillebrand, of recent introduction.

NOTE 30 (page 58)

The Beach-drift of the Hawaiian Islands

It was pointed out by Dole long ago in one of the Hawaiian Club Papers (1868) that the existing currents bring to this archipelago only huge pine logs from Oregon, but no tropical fruits; and Hillebrand (p. xiv.) refers to the driftwood of pine logs from the north-west coast of America, stranded on the shores of these islands. This drift seems to collect in quantity in particular localities, as on the south-east coast of Hawaii between Honuapo and the Kalae promontory (especially on the Kamilo beach near Kaluwalu) and on the east coast of Oahu; and probably there are other favourable localities for catching the drift on the northern shores of Maui and Molokai.

It was on the south-east coast of Hawaii (on the beach at Kamilo and on the eastern side of the Kalae promontory) that this drift came particularly under my notice. Here the logs are stranded in abundance, in sufficient quantity, in fact, to build a town, and they were employed for building purposes by the manager of the neighbouring sugar-cane plantation. Several of the logs are of huge size, as much as 4 feet in diameter; and they are known locally as "white cedar" and "red cedar," and characterised as Oregon timber. Some of them are extensively burrowed by the "teredo" and other boring mollusks. Others recently stranded are covered with barnacles (Lepadidæ), whilst others that have lain long on the beach are bare. I have seen these logs occasionally washed up at Punaluu and at different places on the lava-bound Puna coast. They apparently first strike the Puna coast, and are drifted along until they become embayed near the Kalae promontory, and ultimately stranded. Mingled with them on the beaches Pandanus trunks occur in number; they evidently hail from those parts of the Puna coast where Pandanus forests prevail, and thus they indicate the direction of the drift on the coast of this island. In places there was a considerable amount of small

vegetable *débris*, sometimes partially concealed by the sand, and containing seeds and fruits in fair quantity.

The following seeds and fruits were collected :—

Pandanus drupes, common; most of them fresh-looking, but a few much worn.

Thespesia populnea, a few seeds.

Ipomea pes capræ, seeds, fair numbers.

Ipomea bona nox, seeds, a few.

Ipomea glaberrima, seeds, a few.

Argyreia tiliæfolia, fruits and seeds, a few.

Strongylodon lucidum, seeds, a few.

Cæsalpinia Bonducella, a single seed.

Vigna lutea, seeds, a few.

Calophyllum inophyllum, a few fruits.

Ricinus communis, a few, the seeds either free or in the cocci, and often empty or decaying.

Aleurites moluccana, seeds, common, none sound, either empty or containing a rotten kernel: also a single fruit.

One or two seeds not identified.

There was seemingly a total absence of the fruits or seeds of any littoral plant not found in these islands, such as I was familiar with in the South Pacific. In the mass this seed-drift could have been derived from the neighbouring coasts of the island. This is especially indicated in the cases of the fruits and seeds of Aleurites moluccana, Ricinus communis, and Argyreia tiliæfolia. The sound seeds of Aleurites do not float, the buoyant seeds being always empty, or nearly so; and the presence of the seeds in beach-drift, as explained on page 419, is due partly to the buoyancy of the empty seed and partly to the decay of the stranded fruit, the fruits being able to float for a week or two. So, also, the seeds of Ricinus, whether free or inclosed in the coccus, do not, when sound, float longer than a week or ten days. The capsules of the Argyreia can float two or three weeks, whilst the seeds vary in their behaviour, as observed on page 20. I noticed in places where the vegetable *débris* was heaped up and exposed to the sun's heat, that some of the Ipomea seeds were germinating. It is to be remarked that horse-dung and goat-dung are always common in the beach-drift of these islands. Seeds are sometimes to be seen in the stranded material; and it was evident that the droppings of these animals can float for some weeks before breaking down. . . . I may add that large sponges, apparently of no value, are thrown up in quantities on the east side of the Kalae promontory.

Excepting the pine logs, the only things coming under my notice in this beach-drift that could be characterised without hesitation as non-Hawaiian, were two well-worn pieces of acid pumice, less than an inch in size. One of them was incrusted partially by the tubes of annelids, and both of them had evidently been drifting about in the Pacific for a long period,

perhaps for years. They were such as occur in abundance on the beaches of the South Pacific, and, in fact, on all the shores of the Pacific Ocean, both temperate and tropical. Although I carefully searched the stranded drift of many beaches in this group, no other specimens of drift pumice were found.

On different parts of Oahu the beach-drift was always made up of materials derived from the vegetation of the coast adjacent. Of most frequent occurrence were the seeds of Ipomea pes capræ and Vigna lutea, and the fruits of Scævola Kœnigii, Vitex trifolia, and Pandanus odoratissimus. In addition, the empty seeds of Aleurites moluccana were numerous, and there were occasional seeds of Thespesia populnea, Colubrina asiatica, and Mucuna gigantea. On one beach there were a number of fruits of Terminalia Katappa, showing but little signs of ocean travel, and evidently derived from trees in the vicinity. This tree was introduced by Europeans; but it is not unlikely that in a generation or two it will become, without man's aid, one of the characteristic beach trees of Oahu. It may be remarked that the pods of Acacia Farnesiana, a shrub now growing abundantly in Oahu near the sea, are washed up in great quantities on the beaches of the west coast of this island, and the seeds are to be seen germinating in numbers on the beach, the seedlings striking into the sand. The pods float unharmed in sea-water for four or five weeks, but the seeds, when freed, sink.

Although the above evidence gives no indication of tropical drift of non-Hawaiian origin on the beaches, it is probable, for reasons adduced in Chapter VIII., that, in the winter, drift may be brought from tropical America.

NOTE 31 (page 59)

THE INLAND EXTENSION OF THE SHORE-PLANTS OF HAWAII

Cæsalpinia Bonducella.—According to Hillebrand, this plant, so characteristic of the littoral floras of tropical regions, grows "in gulches of the lower plains on all the islands," no reference being made to its occurrence on the beaches. It is very rarely to be seen on the beaches of the large island of Hawaii; but it is to be found on the lava-bound coasts, and from there it extends inland usually on old lava-flows for five or six miles, and reaches sometimes considerable elevations. In one locality I found it at 2,000 feet above the sea (see page 188).

Cassytha filiformis.—Though a typical shore-plant in Fiji and other tropical localities, it is rarely so in these islands. Hillebrand says nothing of its station. It grows well in the lower open wooded regions, and is frequently found amongst the blocks of old lava-flows near the coast.

Cuscuta sandwichiana.—Unlike its fellow parasite Cassytha filiformis, this species of Cuscuta, which is confined to this group, never came under

my notice away from the beach; and Hillebrand speaks of finding it only at the coast (see page 366).

Ipomea pes capræ, as I observed it in the islands of Hawaii and Oahu, is confined to the beach or to neighbouring sand-dunes. Hillebrand makes no reference to its occurrence inland. This species in these islands offers thus a great contrast to its behaviour in Fiji.

Scævola Kœnigii.—Whilst most at home on the sandy beaches, this plant is also frequently met with in the island of Hawaii on scantily vegetated lava-flows near the coast; but I never noticed it more than a few hundred yards from the sea.

Tephrosia piscatoria.—Though it may occur on the beach, it is generally found as described by Hillebrand on the rocky or rubbly ground at the back of the beach, as well as further inland. It is common on the old lava-fields of the island of Hawaii near the coast; and, according to the natives, its seeds are disseminated by the wild goats that frequent these localities.

Tribulus cistoides.—Hillebrand observes that this plant is found along the sea-shore and on the lower plains. I found it most frequently on the beaches and on the old lava-flows near the sea.

Vitex trifolia, var. unifoliolata.—It is confined, as Hillebrand remarks, to the beaches. Neither in Oahu nor in Hawaii did I ever find it straying inland, which is the more remarkable since this variety, or one closely similar to it, is one of the most characteristic inland plants of the Fijian strand-flora.

Vigna lutea.—This plant was found by me growing on the beaches and in their vicinity. Hillebrand merely speaks of it as "growing at short distances from the shore."

Some of the trees, usually littoral in their station in the tropical Pacific, which are regarded as having been introduced in early times into the Hawaiian group by the Aborigines (see Chapter VII.), behave, nevertheless, quite like indigenous plants in the inland regions and in the lower levels. This is true, for instance, of Hibiscus tiliaceus and Pandanus odoratissimus, the last-named forming forests at the sea-board extending in places far up the mountain slopes. The same, however, may be said of other plants known to have been introduced since the discovery of the islands, as in the cases of Cactus Tuna and of Ricinus communis; and it also applies to Aleurites moluccana, the Candle-nut Tree, which, although it could only have been introduced by the Aborigines, now forms forests on the lower slopes of the mountains.

NOTE 32 (pages 19, 112, 165)

The Fijian Species of Premna

I was much interested in the small trees and shrubs of this genus in Fiji, more especially on account of the relation between the shore and

inland species. This is an Old World genus containing some eighty species mainly characteristic of tropical Asia and Malaya, and represented in the South Pacific archipelagoes by two species, one Premna taitensis or tahitensis, spread over the region and very near P. integrifolia, an Asiatic species; the other Premna serratifolia, an Asiatic plant found in Fiji, the Marquesas, and other groups. Without endeavouring to give a precise value to the Fijian plants, I will merely describe the prevailing forms, which are, however, connected by intermediate varieties. These trees, I may add, are known by the same name in the various Pacific groups, "Avaro" or "Avalo" in Tahiti, "Alo-alo" in Samoa, "Yaro" and "Yaro-yaro" in Fiji.

The Fijian plants may be thus described . . . (*a*) Premna serratifolia, an inland tree, growing in open woods and on the outskirts of the forest, 25 to 30 feet high, more or less hairy, leaves coarsely serrated with long tapering points, putamen prominently tuberculated and thick-walled.

(*b*) Premna taitensis or P. integrifolia, a low straggling coast tree or shrub of the beaches, the coral islets, the swampy borders of the estuaries, and the inland talasinga plains, its usual height being eight to ten feet, except in the inland plains, where it is dwarfed, and three to five feet high. It is more or less glabrous, the leaves being typically entire with obtuse or retuse and mucronate apices. The putamen is thin-walled and relatively smooth. (*c*) Intermediate forms found generally in the inland plains or talasinga regions.

On the Modes of Dispersal.—Speaking generally, the small drupes of both species float at first, but the soft parts are soon removed by decay, and the stone is freed. In the case of the coast species, P. taitensis, the stones float indefinitely and are often found afloat in rivers. In the case of the inland tree, P. serratifolia, most of the stones sink at once, whilst the others sink in a few days. It is probable that currents are one of the effective agencies in distributing the coast species, but this could not apply to the inland tree. The fruits of both the inland and the coast species would attract birds, and the stones would resist injury in their crops. This is the agency advocated by Prof. Schimper for the shore species, P. integrifolia, of Indo-Malaya; and fruits referred with a query to this genus were found in the collection of seeds and fruits obtained by me from the crops of pigeons in the Solomon Islands (*Bot. Chall. Exped.*, Introd. p. 46, part IV. p. 312).

On the Cause of the Buoyancy of the Stone or Putamen of the Coast Species.—This is primarily connected with the empty seed-cavities, the four-celled stone usually developing only one seed, the other cavities being empty. This inference was established by the dissection of a large number of stones, but it will be seen from the table below that one-seeded stones are also frequent in the case of the inland tree (P. serratifolia), where they as a rule sink. With either species the substance of the stone has no floating power, but with the shore species, on account of the thin-walled

stone, the empty seed-cavities cause it to be specifically lighter than water whilst with the inland species the walls of the stone are so thick that the empty spaces of the unfilled seed-cavities do not effect the same result. It may be remarked that when the coast species grows in the inland plains the buoyancy of the stone is preserved.

	One-seeded stones.	Two-seeded stones.	Three-seeded stones.
Inland tree (P. serratifolia)	73 per cent.	23 per cent.	4 per cent.
Coast tree (P. taitensis)	92	8 ,,	—

NOTE 33 (page 63)

De Candolle's List of Plants dispersed exclusively by Currents

Drepanocarpus lunatus; Ecastaphyllum Brownei; Mucuna urens, D.C.; Tephrosia piscatoria; Hibiscus tiliaceus; Rhizophora mangle; Guilandina Bonduc, Linn.; Ipomea pes capræ; Canavalia obtusifolia.

I have experimented on the buoyancy of the fruits and seeds of all these plants excepting the two first named. In five species the seeds float in sea-water unharmed for several months. With Rhizophora it is the floating seedling that disperses the plant. Neither the pods nor the seeds of Tephrosia piscatoria are suited for dispersal by the currents.

NOTE 34 (page 64)

The Littoral Plants of the Easternmost Polynesian Islands

Except in the case of Hernandia peltata my authority here is the *Botany of the "Challenger" Expedition.* Mr. J. H. Maiden gives some further details of the flora of Pitcairn Island in a more recent paper (*Austral. Assoc. Rep.*, Melbourne, 1901, vol. 8), and Hernandia peltata is included in his list.

NOTE 35 (page 68)

Distribution of the Littoral Plants with Buoyant Seeds or Fruits that are found in the Fijian, Tongan, Samoan, Tahitian, and Hawaiian Groups

This list probably contains nearly all the species of the Polynesian region, but it is not implied that these plants have been recorded from all the groups (*vide infra*).

(a) *Species found only in the Old World.*—Calophyllum inophyllum, Hibiscus diversifolius, Thespesia populnea, Heritiera littoralis, Kleinhovia hospita, Carapa moluccensis, C. obovata, Smythea pacifica, Colubrina asiatica, Mucuna gigantea, Erythrina indica, Strongylodon lucidum.

Dalbergia monosperma, Pongamia glabra, Inocarpus edulis, Derris uliginosa, Afzelia bijuga, Barringtonia racemosa, B. speciosa, Rhizophora mucronata, Bruguiera Rheedii, Terminalia Katappa, T. littoralis, Lumnitzera coccinea, Pemphis acidula, Morinda citrifolia, Guettarda speciosa, Wedelia biflora, Scævola Kœnigii, Cerbera Odollam, Ochrosia parviflora, Cordia subcordata, Tournefortia argentea, Ipomea glaberrima, I. grandiflora, I. peltata, Aniseia uniflora, Clerodendron inerme, Vitex trifolia, Hernandia peltata, Excæcaria Agallocha, Tacca pinnatifida, Cycas circinalis, Pandanus odoratissimus, Scirpodendron costatum.

(b) *Species occurring in both the Old and New Worlds.*—Hibiscus tiliaceus, Suriana maritima, Ximenia americana, Dodonæa viscosa, Canavalia obtusifolia, C. ensiformis, Vigna lutea, Sophora tomentosa, Cæsalpinia Bonduc, C. Bonducella, Entada scandens, Gyrocarpus Jacquini, Luffa insularum, Ipomea pes capræ, Cassytha filiformis, Cocos nucifera.

(c) *Species occurring in America to the exclusion of the Old World.*—Dioclea violacea, Mucuna urens, Rhizophora mangle.

(d) *Species found only in Polynesia.*—Canavalia sericea, Mucuna platyphylla (?), Cynometra grandiflora, Serianthes myriadenia, Parinarium laurinum (?), Premna tahitensis.

Remarks.—Of these seventy plants there is not one that has not come within the scope of my observations and experiments. The West Coast of Africa is included in the American region for reasons given in Chapter VIII. For the other authorities on the buoyancy of these seeds and fruits reference should be made to the list given under Note 2 and to other parts of this work. About one or two of the plants, like Ipomea peltata, one scarcely knows whether they are most characteristic of the coast-flora or of the inland-flora.

NOTE 36 (page 72)

Hawaiian Plants with Buoyant Seeds and Fruits known to be dispersed by the Currents either exclusively or, as in a few Species, with the Assistance of Frugivorous Birds

Colubrina asiatica.—Usually regarded as confined to the Old World; but since nearly all the species are American, that continent may be considered as the probable home also of this species. Hillebrand gives it a locality in the West Indies.

Dioclea violacea.—Tropical America.

Mucuna gigantea.—Old World.

Mucuna urens.—America, and extending to the African West Coast, which is to be included in the American region of shore-plants.

Strongylodon lucidum.—Old World.

Vigna lutea.—Old and New Worlds.

Cæsalpinia Bonducella.—Old and New Worlds.

Scævola Kœnigii.—Usually regarded as confined to the Old World, but

according to the synonymy accepted by some authors it is also to be ascribed to America. The genus is chiefly Australian, and it is possible that the littoral species may have reached America through the agency of birds, since all the species of the genus possess fruits that would attract frugivorous birds.

Ipomea glaberrima (Boj.).—Old World.

Ipomea pes capræ.—Old and New Worlds.

Vitex trifolia.—Old World. The genus is also dispersed by pigeons.

Cassytha filiformis.—Old and New Worlds. Like Scævola the genus is chiefly Australian, and here, also, the fruits of the littoral species are not only dispersed by the currents, but are known to be also disseminated by fruit-pigeons.

It is possible that birds may have taken a predominant part in the dispersal of the species of Scævola, Vitex and Cassytha.

There thus remain nine species for consideration. Of these two are exclusively American, three are found in both the Old and New Worlds and four are usually regarded as exclusively Old World plants, but one of them (Colubrina asiatica) has a fair claim to be regarded as of American origin. Thus it is quite possible that six out of these nine plants were brought to Hawaii from America through the agency of the currents.

NOTE 37 (page 78)

On Vivipary in the Fruits of Barringtonia racemosa and Carapa obovata

As observed by me in the Rewa delta, Fiji, there was no external evidence of such a process in the case of the fruits on the trees; but I did not pay very special attention to the matter, and it will be gathered from Chapter XXX. that the initial stage of germination may show no indication in the appearance of the fruit. More observation is needed for both species. As indicated in Note 50, the structure of the seed of Barringtonia racemosa is suggestive of a lost viviparous habit. With regard to Carapa, Schimper (p. 43) remarks that he has never observed vivipary; but Miquel, in his *Flora Indiæ Batavia*, particularly speaks of the seeds germinating in the capsule. I think this is very likely, and that perhaps even the rupture of the capsule may be partly due to this cause.

NOTE 38 (page 78)

On the Temperature and Density of the Surface-water of the Estuaries of the Rewa River in Fiji, and of the Guayaquil River in Ecuador

(a) *The Rewa Estuary.*—My observations were made mostly in the warm, wet seasons, from October to January, 1897–99, and generally in

the vicinity of the Roman Catholic Mission. The density varied usually between 1·000 and 1·010, the water being quite fresh after heavy rains inland. Though the density was usually greatest at high water, this was by no means always the case. The temperature of the water in dry weather varied from 79° to 84° F. With the river in flood after heavy rains it fell to 75° and 76°. As a rule, the fresher the water the lower the temperature, but this was not invariable. There was evidence of super-heating in the estuary, the water there having sometimes a temperature of 82° or 83°, when the water higher up the river as far as Viria was two or three degrees cooler, the sea-temperature being 79° to 80°. The average temperature of the water of the estuary during the season would be 80 to 81°.

(b) *The Estuary of the Rio Guayas, also known as the Guayaquil River.*—My observations were made in the last week of February and in the first half of March, 1904. Whilst the sea-temperature a few miles off the Ecuador coast varied from 76° to 80° F., the water of the estuary from the mouth up to Guayaquil ranged from 79° to 86°, whilst rather higher up the river the temperature was about 79° or 80°. The super-heating of the estuary is thus directly indicated. It was well marked in the lower part of the estuary during one of my ascents of the river.

Surface-temperatures of estuary of the Guayaquil River, March 13, 1904, 11 a.m. to 4 p.m.; tide running up.	Sea-temperature 5–10 miles off the mouth	79·7
	Estuary-temperature at the mouth, off Puna	82·7
	,, ,, 3 miles above ,,	84·4
	,, ,, 15 ,, ,, ,,	86·5
	,, ,, 25 ,, ,, ,,	82·5
	,, ,, off Guayaquil	81·8

The water of the estuary was, as a rule, cooler with the ebbing tide.

The density of the estuary-water at the mouth opposite Puna during the two days the ship was in quarantine ranged from 1·004 to 1·016, being generally about 1·010, and salter with the up-going tide. Off Guayaquil the water during the ebbing tide was quite fresh and, from an Ecuadorian standpoint only, potable, whilst at high water it may be a little brackish. The sea-water has much freer access to the channels in the mangrove-district at the back of the city of Guayaquil, where at high water I found the density to be 1·014.

Off Puna, on Feb. 25, I noticed that the surface-current which was running down the stream was from one to two fathoms deep, whilst below it was a strong current running up the river which carried my thermometer up against the surface-current.

NOTE 39 (page 82)

On the Pacific Species of Strongylodon

Hillebrand in his *Hawaiian Flora*, following Seemann, regards S. lucidum, Seem., and S. ruber, Vogel, as one species found in Fiji.

Hawaii, and Tahiti, and by the former placed also in Ceylon. Hillebrand and Seemann are followed by Drake del Castillo as regards the Tahitian species. Taubert, in his monograph on the Leguminosæ (Engler's *Pflanz. Fam.*, Teil 3, Abth. 3, 1894), takes the same view of the Polynesian species and of its wide distribution. However, in the *Genera Plantarum* and in the *Index Kewensis*, the Asiatic and Polynesian species have been always kept apart. The two species of the genus mentioned in the first work are increased to five in the *Index Kewensis*, viz., one in Fiji (S. lucidum), one in Hawaii (S. ruber), two in Madagascar, and one in the Philippines.

NOTE 40 (page 88)

Precautions in Testing Seed-buoyancy

Many seeds and fruits require a few hours' soaking before they sink; and when small they will rest a long time on the surface of still water, but a touch with the finger or a drop of water will send them to the bottom. A few will float a few days (3 or 4) before sinking; but such are included in the non-buoyant group. Only in rare cases does prolonged drying increase the period of flotation by more than a few days, examples being given at the end of the Table of Buoyancy results under Note 10. Adherent air-bubbles, a common cause of adventitious buoyancy, must always be removed.

NOTE 41 (page 91)

The Buoyancy of the Seeds of Convolvulus Soldanella in Fresh Water and Sea-water compared

The experiments were commenced at the close of September, 1894, and covered six months. At the end of this period in Mr. Millett's experiment, 56 per cent. of the seeds were afloat in fresh water, and 62 per cent. in sea-water; whilst in my own experiment 72 per cent. floated in fresh water, and 65 per cent. in sea-water. I was indebted to Mr. Millett's courtesy for the seeds.

NOTE 42 (page 96)

On Secular Changes in Sea-density

Exact data bearing on this subject are not at my disposal; but it would seem that geologists have formed conflicting conclusions from similar premises. There is the view that the composition of the ocean water was very different in early geological periods (*Encycl. Brit.*, x., 221); but I should imagine that the character of the crustacean fauna of those seas would negative any great divergence from the present condition. Suess implies that the ancient seas carried the same minerals in solution that they do now, and it is to be inferred in a similar proportion (E. de Margerie's French edition of *Das Antlitz der Erde*, ii., 343 and 345)

NOTE 43 (page 102)

On the Mucosity of Small Seeds and Seed-like Fruits when wet

I paid considerable attention to this subject from the standpoint of dispersal some years ago, and published most of the results in *Science Gossip* for Sept., 1894. This peculiar quality of seeds had been noticed by Dr. Kerner in his *Pflanzenleben* (vol. i., 1887–91), and was regarded as illustrating a mode of dispersal of seeds by adherence. As a rule, such seeds when placed in water become coated with mucus in a few minutes, or within an hour, and when allowed to dry on feathers they adhere as firmly as if gummed. I found that this quality is not affected by prolonged drying, as in the cases of Nepeta glechoma and Salvia verbenaca, where it was exhibited to the same degree after the seed-like fruits had been kept from one to three years. I especially tested about 110 British plants that were likely to display this quality, and found that about a dozen exhibited it in a marked degree, and if to these we add those plants with seeds that display it to a limited extent so that they merely become adhesive when wetted, the total would be nearly twenty. It will be noticed from the list subjoined that the plants showing marked mucosity belong to twenty genera and to ten families, the Labiatæ and Cruciferæ predominating. Although in some genera, like Plantago, there is reason to suppose that the seeds of all the species would behave in this fashion, it would be wrong to infer that this is usually the case, six genera being indicated below to which such a rule would not apply, and doubtless the number could be extended. These plants in England mostly occur at the roadside, on waste ground, and in dry meadows. It may be added that although in most cases the seeds appear in water to emit mucus, "exuded mucilage" being the expression used in the English edition of Kerner's work, in some instances, as with Helianthemum vulgare, there appears to be a dissolving process affecting the outer seed-covering.

I. *Plants with Seeds or Seed-like Fruits that emit Mucus to a Marked Degree when placed in Water.*

Arabis thaliana, G.	Cruciferæ.
Camelina sativa, K.	
Teesdalia, K.	
Capsella bursa-pastoris, G.	
Lepidium sativum, D.	
Helianthemum vulgare, G.	Cistaceæ.
* Viola tricolor (Field Pansy), G	Violaceæ.
Linum usitatissimum, D.	Linaceæ.
Linum, K.	

* Matricaria chamomilla, K. G. } Compositæ.
* Senecio vulgaris, G. B.

Collomia, K. } Polemoniaceæ.
Gilia, K.

* Veronica beccabunga, S. Scrophulariaceæ.

Ocimum basilicum, K. } Labiatæ.
Salvia verbenaca, G., &c.
Salvia, K. B.
* Nepeta glechoma, G.
* Dracocephalum, K.
Prunella vulgaris, G.

Plantago, K. } Plantagineæ.
Plantago major, lanceolata, maritima, G.

Luzula campestris. G. Juncaceæ.

Explanation of Abbreviations.—The capital letter following the name indicates my authority, which is not necessarily the oldest in each case: B = Beal; D = Darwin; G = Guppy; K = Kerner; S = Scott Elliot. The respective works quoted will be found at the end of this volume. The papers of Darwin quoted will be found in *Journ. Linn. Soc.*, "Botany," vol. i., 1857, and in the *Gardener's Chronicle* for 1855.

The asterisk is placed before those genera of which other species examined by me exhibited no mucosity; these species are Arabis hirsuta, Viola canina, V. palustris, Matricaria inodora, Senecio aquaticus, Veronica agrestis, V. arvensis, Nepeta cataria, Dracocephalum canariensis.

II. *Plants with Seeds or Seed-like Fruits which in my Experiments only exhibited Mucosity in a Slight Degree, becoming merely "Sticky" or Adhesive when placed in Water.*

Arabis albida, Chrysanthemum leucanthemum, Lamium purpureum (occasionally), Thymus sp., Juncus bufonius, J. communis, J. glaucus, J. squarrosus.

III. *Plants with Seeds or Small Fruits that exhibit Adhesiveness in the Dry State and are apt to stick to one's fingers.*

Adenostemma viscosum, Lycopus europæus, Piper Macgillivrayi, &c. One may include here also Lagenophora (see page 276) as well as the familiar instances of Pisonia (page 347) and Boerhaavia (page 356).

NOTE 44 (page 121)

On the Effects of Inland Extension on the Buoyancy of the Seeds or Fruits of Littoral Plants

When in Fiji I experimented on the buoyancy of the following beach-plants that had extended far into the interior of Vanua Levu, as will be

found described in Note 22. Those tested were Cassytha filiformis, Cerbera Odollam, Ipomea pes capræ, Morinda citrifolia, Premna tahitensis, Scævola Kœnigii, and Tacca pinnatifida. In all but Cerbera Odollam, where I contented myself with establishing that the fruits floated buoyantly in sea-water, the experiments were prolonged for many weeks and often for several months; and in some cases, as with Ipomea pes capræ, three or four experiments were made on seeds from different inland localities. The result was to establish in all cases that the floating powers were as great with the inland as with the coast plants of the same species; nor could any structural difference of importance be noticed. It should be observed that there is every reason to believe that the "talasinga" plains of Fiji have been occupied by the intruding beach-plants for many ages.

NOTE 45 (page 122)

TABULATED RESULTS OF THE CLASSIFICATION, ACCORDING TO SCHIMPER'S APPLICATION OF THE NATURAL SELECTION THEORY, OF THE BUOYANT SEEDS AND FRUITS OF THE TROPICAL LITTORAL PLANTS ON THE BASIS OF THE STRUCTURAL CHARACTERS CONCERNED IN BUOYANCY

Region.	Classification of species.						Proportion of non-adaptive and adaptive species.		Total number of species dealt with.
	Non-adaptive.				Adaptive.				
	First group.		Second group.		Third group.				
	Number.	Per cent.	Number.	Per cent.	Number.	Per cent.	Percentage of non-adaptive species.	Percentage of adaptive species.	
Pacific Islands	27	40	10	15	30	45	55	45	67
Pacific Islands, tropical America, and Indo-Malaya	28	35	12	15	40	50	50	50	80

NOTE.—If to the last we add the eight British shore plants, the buoyant fruits of which are described in Chapter XII., three non-adaptive and five adaptive, we get a proportion of adaptive species for temperate and tropical regions of fifty-one per cent. This is probably fairly typical of the world generally; but it must be remembered by the reader that the author regards them all as non-adaptive. In that case, the table can be used for the numerical results of the three groups which are based only on structural characters without reference to any theory.

NOTE 46 (page 124)

ON THE MODES OF DISPERSAL OF THE GENUS BRACKENRIDGEA.

Seed-vessels of this genus found afloat in the New Guinea drift are described by Mr. Hemsley as having two curved cavities crossing each other, one containing a seed, the other empty. "This empty cavity," it is stated, "gives the fruit its buoyancy" (*Bot. Chall. Exped.*, iii., 289; plate 54). Dr. Beccari, in the English edition of his *Wanderings in Borneo*, p. 187,

speaks of the closed air-containing cavities in the seed-vessels, or rather "stones," of this genus as probably giving them buoyancy and thus enabling them to be dispersed by currents. He points out that the fleshy covering of these fruits would also aid their dispersal by birds. The Italian botanist implies that the two Bornean species grow in swamps. The Fijian species, as observed by me in flower in Vanua Levu, grew in the dry talasinga districts bordering the Mathuata coast, the locality where Seemann found the plant. One of the most recent accounts of the genus is given by Van Tieghem in his memoir on the Ochnaceæ in *Ann. des. Sci. Nat. Bot.*, tome 16, 1902. According to him there are nine species, all from Malaya and New Guinea, with the exception of one in Fiji. Previous authors have also referred to Queensland and Zanzibar species. However, all the species have a limited distribution, a fact which plainly assigns to birds the principal share in the dispersal of the genus.

NOTE 47 (page 125)

On the Transport of Gourds by Currents

Small calabashes or bottle-gourds are not uncommonly to be found floating in the Fijian estuaries and stranded on the beaches; and I have also found them in the sea off the coasts. They are usually more or less globular, 3 or 4 inches across, and are evidently able to float for very long periods and to carry the seeds unharmed. Most of those I examined from the drift were dry inside and contained the seeds dried together into a loose ball about an inch in size. The seeds are not those figured in Gaertner's *De Fructibus et Seminibus*, as belonging to Lagenaria vulgaris, and more resemble those of Cucurbita, but are non-buoyant. One of these gourds, picked up by me in the sea in Fiji, was placed in sea-water, and two months later was still floating buoyantly. After being then kept dry for seven months, it was broken open; and ten of the seeds were put in soil, two of them germinating in a few days.

In Ecuador gourds similar in size and shape were frequently observed by me floating in the drift of the Guayaquil River and stranded on the sea-beaches. The seeds are similarly caked together in a loose mass in the cavity of the fruit. Their characters indicate that they belong to another species of gourd; and they differ also from the Fijian seeds in their buoyancy, some of them in my experiments floating two months and afterwards germinating.

It has been known since the days of Ström and Gunnerus, two Norwegian naturalists of the 17th century, that gourds and calabashes are from time to time stranded with other Gulf-stream drift on the coasts of Norway. We learn from Sernander that those found are usually worked calabashes; but he alludes to one that was unworked and contained several seeds (see Sernander, p. 119).

It is scarcely likely that a seed-carrying gourd stranded on a beach would be able to establish the plant without the aid of man; but it seems highly probable that gourds have often been introduced into new countries by the currents and that man has afterwards cultivated them. These plants may be contrasted with that remarkable Cucurbit, Luffa insularum, a genuine littoral plant, the seeds of which, and not the fruits, are dispersed in the Pacific by the currents (see page 426).

NOTE 48 (page 126)

On the Useless Dispersal by Currents of the Fruits of the Oak (Quercus robur) and other Species of Quercus, and also of the Hazel (Corylus avellana)

The fruits of different species of Quercus are of not infrequent occurrence in the seed-drift both of the temperate and tropical regions, being brought down by the rivers to the sea and then stranded on the neighbouring beaches. They were amongst the drift gathered by Mr. Moseley in the open sea, 70 miles off the New Guinea coast (*Bot. Chall. Exped.*, iv., 294). I found them on the beaches of Keeling Atoll where no oak exists, and on the beaches of the south coast of Java; whilst Prof. Schimper noticed them among the stranded drift of the Java Sea, and Prof. Penzig found them stranded on the shores of Krakatoa. They also came under my notice on the Sicilian beaches and on the Italian coast at Cumæ. Those of Quercus robur are to be found on the English beaches and in the autumn drift of the Thames, but they soon sink and disappear from river-drift. They are referred to by Dr. Sernander as frozen with other floating seeds in the ice of the Scandinavian rivers; but he evidently does not regard them as possessing much independent floating power.

Some years ago the author made a number of experiments on the buoyancy of the acorns of Quercus robur, and he formed the conclusion that when freshly collected not more than 4 to 8 per cent. of mature fruits will float in fresh-water, and not more than about 10 to 12 per cent. in sea-water, but that in either case they all sink in a day or two. Immature acorns float much longer, and it is these that mostly figure in the drift. However, unlike most fruits of little initial buoyancy the mature fruits gain considerable floating power by drying. Of some that had been kept for seven months 20 per cent. floated after four weeks in sea-water and 15 per cent. after 10 weeks. . . . It may be added that, according to Thuret, the fruits of Quercus ilex have little or no floating power.

The buoyancy of the fruits of Quercus is due entirely to the cavity left by the shrinking of the kernel. I never remember to have found one with a sound seed amongst the drift in England and Sicily; and I should doubt much whether those in the tropical drift retain their germinating powers.

But, apart from this, the genus Quercus finds in its own constitution or habit the greatest obstacle in most species to the adoption of a littoral station. However, there are exceptional tendencies displayed by the evergreen oaks; and this is very significant, since in their xerophilous leaves they possess the preliminary qualification for a station near the sea. Quercus ilex, it is well known, shows a partiality for the sea-air, and Q. virens, the "live oak," flourishes near the sea in the southern states of America, a maritime variety being distinguished by botanists. One of the willow-oaks of America, Q. phellos, which grows in swampy land, also has a beach variety.

The Hazel-tree (Corylus avellana) must be placed in the same category with Quercus. I found the empty nuts commonly amongst the stranded drift of the Sicilian and English beaches. The fruits were also frequently noticed by Dr. Sernander in the Scandinavian sea-drift; but he says nothing of their empty condition. Mr. Darwin remarks, in the *Origin of Species*, that he found that fresh hazel-nuts sank, but that after drying a long time they floated for ninety days and subsequently germinated. The floating-power is no doubt due to the cavity arising from the shrinking of the kernel, and it is to this cause that Dr. Sernander attributed the slight initial buoyancy observed by him. However, the hazel, like the common oak, lacks the habit that would fit it for a station by the sea, and, whatever capacity its fruits may possess for dispersal by currents, it is quite useless for the spread of the species.

NOTE 49 (page 131)

On the Distribution of Ipomea pes capræ, Convolvulus soldanella, and Convolvulus sepium

Whilst Ipomea pes capræ is cosmopolitan in the tropical zones, Convolvulus soldanella is cosmopolitan in both the north and south temperate zones; but, as might be expected, the two species at times meet and their areas overlap. Thus, according to Mr. Cheeseman (*Trans. New Zealand Inst.*, xx., 1887), they meet in the Kermadec Islands, in the South Pacific, in about latitude 30°. From my observations on the coast of Chile it would seem that C. soldanella in its northward extension fails somewhere between Valparaiso and Coquimbo, that is to say, between 33° and 30° S. lat. Gay merely refers to the plant as existing in North Chile, which in his time would include the coast between 33° and 24° S. lat. It intrudes within the "thirties" on the coast of California and is found in Madeira in about 33° N. lat. Ipomea pes capræ in its turn extends into subtropical regions, being recorded from the Kermadecs, as above noted, and from the Bermudas in 32° N. lat. Owing probably to special physical conditions of the coast, which are referred to in Chapter XXXII., this plant is evidently limited to the tropics on the west coast of South America. It did

not come under my notice on the beaches of North Chile, and it is apparently not mentioned by Gay in his work on the Chilian flora.

Convolvulus sepium, the frequent inland associate of the littoral C. soldanella over the temperate regions of the globe, belongs to the same section of the genus (Calystegia). Its extraordinary occurrence by itself in the island of St. Paul, in the Southern Ocean, about fifty yards from the shore (*Bot. Chall. Exped.*, ii., 153, 264), almost suggests that we have here a dimorphic species with a littoral and an inland form; and its existence in the Azores is in this connection very remarkable. It may be here noted that of three plants raised from seeds found in the beach-drift near Palermo two had the foliage of C. sepium and one of C. soldanella. Perhaps one of my readers, in imitation of De Vries with Œnothera, might be able to settle this point by raising some hundreds of seedlings from the seeds of the beach species. It is possible that the relation between these two species of Convolvulus may be in some respects akin to that between Cæsalpinia Bonducella and C. Bonduc, two littoral plants that accompany each other over much of the tropical zone.

The student of dispersal will, however, find some curious gaps in the distribution of Convolvulus soldanella even in the temperate regions; and it will be curious to observe how they affect the distribution of C. sepium. He will have to answer the query of De Candolle: . . . "Admitting, if one wishes, that the currents have transported this marine species, how comes it that it chances to be in the Pacific and in Europe, without occurring on the east coasts of America and on the east and west coasts of Africa?" (*Geographie Botanique*, ii., 1056). He will have to explain why some botanists give C. soldanella a habitat in the tropics, as in the Indian region. Schimper, who investigated this point, says that he arrived at no certain result (p. 127). See Notes 13 and 41 and pages 29, 91, for further remarks on these two species of Convolvulus.

NOTE 50 (pages 79, 132)

On the Structure of the Seeds and Fruits of Barringtonia

As regards the fruits and their coverings, the littoral and inland species of Fiji evidently fall into different sections, the first named (B. speciosa and B. racemosa) being distinguished by their outer fibrous husk, to which the buoyancy is due, the last-named (B. edulis and an undescribed species) possessing a hard stone surrounding the seed, and here the fruits sink or float only for limited periods.

The fruits of B. edulis have an outer almost fleshy covering, a little fibrous at the outside, and the hard ligneous "stone," containing an edible seed, requires a hammer to break it. They float heavily for three or four weeks, whereas those of the littoral species float for many months. In the case of another inland species found by me growing as a small tree 12 feet

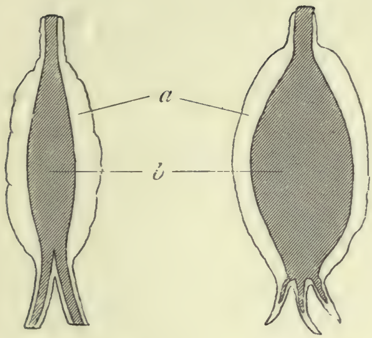
high on the slopes of Mount Seatura in Vanua Levu at an elevation of 1,000 feet above the sea, the seed was similarly protected by a hard "stone" that could only be broken with an axe, and the fruit was non-buoyant, with thin and perishable outer coats.

This mountain species of Fiji, which I may name Barringtonia seaturæ, has the general habit of B. racemosa, with which the natives persisted in linking it; whilst the fruit and foliage come nearer to those of B. edulis. The leaves are entire, taper at the base, and have a petiole 1 inch long. The fruits are oblong, at least 3 inches in length, and are obscurely angled.

It would appear from Schimper's description (p. 173) that the fruits of the Malayan Barringtonia excelsa possess both the hard stone-shell of the inland Fijian species and the dry air-bearing fibrous husk of the littoral species. This is of special interest, since the tree is both a coast and an inland species.

The following notes on the structure of the seeds of Barringtonia were made whilst I was drifting about in my canoe in the creeks of the Rewa delta in Fiji; and whatever may be their deficiencies they have the merit of having been written in the home of the plants. . . . When we cut across a seed like that of B. racemosa or B. speciosa, we observe that the different parts of the embryo are indistinguishable, being united into a homogeneous, firm, fleshy mass. But if we look closely we notice a central fusiform portion marked out from the surrounding parts by a faint line, along which a delicate membrane of vascular tissue has been developed. When "germination" begins, though, as the reader will subsequently perceive, this term is here hardly appropriate, the real nature of this singular structure becomes more apparent, as is indicated in the accompanying figure. The central fusiform portion proves to be the young plant without cotyledons and growing at either end to form the root and the stem. The delicate investing membrane becomes thicker and more apparent as germination proceeds, extending upwards and downwards with the growth of the stem and root and forming a cortical covering in either case. The investing fleshy portion of the seed, which is now separable with the fingers, remains attached to the lower part of the seedling for some time, being evidently a source of nutriment, and gives a bulbous appearance to the young plant. Young bulbous plants of B. racemosa, 1 to 2 feet high, are very common on the edge of Fijian mangrove swamps where the parent tree thrives. The seedlings of B. speciosa have the same appearance, but the outer fleshy part of the bulb is not so thick.

This structure of the seeds of Barringtonia speciosa and of B. racemosa was for a long time meaningless to me, until one day, whilst seated on the banks of the Lower Rewa, with a number of the sected seeds and bulbous seedlings gathered around, I reflected that the fruits of the latter species that floated past me in the river-drift were nearly always germinating. This called up "vivipary" to my mind; and as I looked at the Rhizophora seedlings dangling from the branches of the mangrove-trees close by, it



Diagrams illustrating the structure of the growing seeds of Barringtonia (two-thirds the natural size). That of B. speciosa represents a seed removed from a fruit displaying the young plant protruding two or three inches. That of B. racemosa represents the lower end of the seedling when the plant is eighteen inches high.

a = the exorhiza.

b = the neorhiza invested by the medullary sheath.

occurred to me that this seed-structure might be the result of a lost viviparous habit. One apparently had to deal here not with an ordinary seed containing an embryo in the midst of albumen, but with a seed in an arrested stage of germination surrounded by a body that might perhaps prove homologous with the "cotyledonary body" of Rhizophora. The process of development that goes on without a break in Rhizophora, from the fertilisation of the ovule to the detachment of the seedling from the branch, was here, as I considered, arrested after germination had begun, but before the protrusion of the seedling from the fruit. With nearly all plants, as I reflected, there is a rest-stage of varying length, which might be called the seed-stage. With the mangrove-genera, Rhizophora and Bruguiera, I had convinced myself by a long series of observations, the results of which are given in Chapter XXX., that this rest-stage does not exist. It occurs, I argued, in Barringtonia, but only after germination has begun, and, therefore, displaced when compared with the typical seed-stage of most plants.

In this connection it may be noted that a difference in germinating behaviour might be expected between the two shore species on account of their difference in stations, Barringtonia speciosa growing on the sandy beach, and B. racemosa in the wet ground around a mangrove-swamp. There is a strong suspicion that the rest-stage in B. racemosa is very short, though I never found germination in progress on a tree (see Note 37). There is no doubt, on the other hand, that the rest-stage of B. speciosa is often, as with most other plants, very long. This, then, was my lesson from the Barringtonia fruits on the banks of the Rewa, and the question arose whether this interpretation of these curious seed-structures accorded with the opinion formed of their nature by botanists.

Curious seed-structures of this kind must have their significance in the history of the plant; and on returning to England I looked a little further into the matter. To follow up this kind of inquiry, however, would carry me far beyond the limits prescribed for this note, and I have only treated it here in a tentative fashion. Different botanists of eminence have paid attention to this subject, amongst them Roxburgh, Thomson, and Miers (see Dr. T. Thomson in *Journ. Linn. Soc. Bot.*, vol. ii., p. 47, 1858, and Mr. J. Miers in *Trans. Linn. Soc. Bot.*, vol. i., 1880). It would appear that the seed-structure of Barringtonia is also found in Careya, a genus of the same Myrtaceous tribe, and in Garcinia and other genera of the Guttiferæ, as well as in other inland plants.

Mr. Miers, after reviewing the opinions of his predecessors, gives the results of his own investigations. The solid embryo found in Barringtonia and many other genera consists, he observes, (*a*) of an external portion, the "exorhiza," which nourishes the germinating seed and then dies away; (*b*) of an internal portion, the "neorhiza," which, growing at each end, forms the central portion of the stem and root; and (*c*) the "medullary sheath" of Mirbel, that lies between the two, and is composed of elementary vascular tissue, which ultimately gives origin to the wood, bark, and

leaves of the stem and yields woody fibre to the root. The exorhizal portion in some cases, as in Barringtonia acutangula, splits into four parts during germination. Mr. Miers compares this seed-structure with that of Rhizophora, employing the same terms, "neorhiza" for the internal portion which forms the seedling, and "exorhiza" for the external portion which merely nourishes it. However, I may add that the exorhizal portion in Rhizophora, as shown in Chapter XXX., is now regarded as formed by the coalesced cotyledons, and is termed the "cotyledonary body"; so that by implication the corresponding part of a Barringtonia seed should be regarded from the same standpoint.

It may be apposite to notice here that Barringtonia racemosa displays one capacity which does not appear to belong to B. speciosa. The branches stuck in wet soil throw out roots and establish themselves. This capacity of vegetative reproduction is turned to account by the Fijians, who make "live-fences" of this tree in wet localities.

NOTE 51 (page 135)

On a Common Inland Species of Scævola in Vanua Levu, Fiji

This is a tall shrub, or small tree, nine or ten feet high, which corresponds with S. floribunda, Gray, as far as Seemann describes it. It has small, black, juicy drupes, well suited for dispersal by birds, having no "suberous" mesocarp as in the shore species (S. Kœnigii), and no capacity for dispersal by currents. It grows, much like the Hawaiian inland species, in exposed situations where there is plenty of light, as on mountain-peaks, at the borders of forests, in open-wooded districts, and in the plains, and is to be found at all elevations from near the sea up to the highest mountain summit (3,500 feet) when the station is suitable. I noticed it on the higher slopes and frequently on the tops of nearly all the principal mountains that I climbed. It is evident that birds carry the "stones" from one mountain-peak to another, and no doubt they explain the presence of the species in Tonga. Dr. Seemann speaks of it as a beach plant in Viti Levu. The plant familiar to me in Vanua Levu is only on very rare occasions to be seen as an intruder in the beach-flora.

NOTE 52 (page 137).

On the Capacity for Dispersal by Currents of Colubrina oppositifolia, an Inland Hawaiian Tree

The seeds in my experiments sank within ten days; but they are not readily detached from the fruit, as in the case of the buoyant seeds of the littoral species (C. asiatica). The fruits, which may float for a week or two, break down, as Hillebrand observes, tardily and imperfectly, and could give but little assistance to dispersal by water.

NOTE 53 (page 141)

On the Genus Erythrina

We have in E. indica a widely distributed littoral species, ranging from India through Malaya to eastern Australia, and over nearly all the groups of the Pacific, reaching to Tahiti and the Marquesas, but not occurring in Hawaii. It is associated in Fiji and Tonga with another shore-species, E. ovalifolia, Roxb., found also in India and Malaya. I did not come on the second species in Fiji, and according to Seemann it is rare. It is possible that there is a genetic connection between the two; and it is noteworthy that in one case Seemann was uncertain (p. 426) whether the species was E. ovalifolia or only a variety of E. indica.

In different parts of their areas both these species may be found inland. This no doubt is to be connected with their occasional cultivation. The Polynesians who esteem E. indica for its handsome scarlet flowers and its scarlet seeds often plant it near their houses; but it is curious that if we look at the pages of Seemann, Horne, and one or two other botanical authors who have written on the Pacific, we find no reference to its littoral station, the first-named botanist merely characterising it in Fiji as occurring "wild or planted."

However, in various localities in Fiji, as on the shores of Natewa Bay in Vanua Levu, Erythrina indica thrives as a characteristic beach tree. Dr. Reinecke speaks of it as widely spread on the Samoan coasts; and the French botanists refer to it as a tree of the Tahitian beaches. Prof. Schimper frequently mentions the two littoral species of Erythrina as amongst the components of the Malayan strand-flora. Dr. Treub, when he visited Krakatoa in 1886, three years after the eruption, noticed some young plants of Erythrina growing on the shore; whilst Prof. Penzig in 1897 found that both E. indica and E. ovalifolia had established themselves on the beach. Mr. Kurz again is quoted by Prof. Schimper (p. 170) as including E. indica amongst the "beach-jungle" of Pegu.

There is abundant evidence in support of the dispersal of the genus by currents. I have observed the seeds of Erythrina indica on the beaches of Keeling Atoll. Schimper noted Erythrina seeds amongst the stranded drift of the Java Sea. Treub remarked young plants of the genus growing on the shore of Krakatoa three years after the great eruption, and Penzig places Erythrina indica and E. ovalifolia amongst the beach-plants brought to Krakatoa through the agency of the currents. The seeds of E. indica not infrequently came under my observation stranded on the Fijian beaches and floating in the Rewa estuary; and in an experiment made in Fiji they still floated after five months in sea-water. Mr. Hemsley years ago formed the opinion, from the drift collections at Kew, that the genus was dispersed by the currents. I may here add in further illustration of this point that Erythrina seeds were found by me in South America

floating in numbers in the Guayaquil estuary and stranded on the beaches of Ecuador.

It is noteworthy that, unlike some of the other shore-plants, Erythrina indica has at least three sets of names in the South Pacific. Thus it is known as Rara and Ndrala in Fiji, Ngatae in Samoa, Futuna, and Rarotonga, Atae in Tahiti, and Kenae in the Marquesas. The Samoan and Tahitian name recalls the Burmese name of Ka-thit, whilst the Marquesan word is suggestive of the Makassar name Kăne or Kanur. The Hawaiian name of E. monosperma is Wili-wili, which evidently has arisen from the screw-like movement of the open pod when thrown into the air. The same name in the form of Wiri-wiri is applied for a similar reason to Gyrocarpus Jacquini in Fiji. It is possible that the Polynesians have assisted the dispersal of the coast-species (E. indica); but the currents could have performed the distribution unaided, and the variety of aboriginal names is not in favour of human intervention.

With reference to the possible extermination by insects of Erythrina in Hawaii, it has been before remarked (p. 143) that this would not account for the survival of an inland species, such as E. monosperma in Hawaii. However, this species since the occupation of that group by the white man is on the road to extinction. Dr. Hillebrand observes that the species was much more common formerly than in his time (1851–1871), a result evidently due to the ravages of the common tropical mealy bug, a pest of relatively modern introduction (see Koebele in Stubb's *Agricultural Report on Hawaii*). It may be added here that Cordia subcordata, a littoral tree, had been almost exterminated by the ravages of a small moth even in Dr. Hillebrand's time. During my examination of the coasts of the large island of Hawaii, in 1896–7, I was shown several places not long before occupied by this tree; and, as indicated in Note 29, it only came under my notice in a few localities.

NOTE 54 (page 145)

On the Genus Canavalia

Of the three maritime species, C. obtusifolia, D.C., occurs on beaches all round the tropical zone. I was familiar with it on North Keeling Island in the Indian Ocean, in Fiji, and in Ecuador. C. ensiformis, D.C., is just as widely spread; but it is both inland and maritime in its station, and except when collecting it in the Solomon Islands I have had but little acquaintance with it. C. sericea (Gray) is a characteristic beach-plant in Fiji, but is infrequent. In Rarotonga, according to Cheeseman, it is a common littoral plant. It was also found in Tahiti by Banks and Solander, and is seemingly peculiar to the Pacific islands.

Besides C. ensiformis, the other two shore species may at times be found inland. Thus it is singular that the French botanists do not, as a rule, speak of C. sericea as a Tahitian beach plant; and Nadeaud only

remarks, concerning its station, that it frequents the wooded slopes of the valleys of the interior. In North Keeling Island C. obtusifolia presented itself to me not only as a beach-creeper, its usual habit, but as a climber over the branches of the coast trees. In one locality in Vanua Levu I found a variety of this species growing on a hill a mile inland and about 700 feet above the sea. On one of the beaches it approached C. sericea in some of its characters, as in the form of the calyx and in the hairiness.

Although the seeds of C. obtusifolia have long been known to be dispersed by the currents, having been found in Moseley's collections of floating drift off the New Guinea coast (*Bot. Chall. Exp.*, IV, 291), they displayed remarkable fickleness when experimented on by me in Fiji. As a rule, however, about 10 per cent. sank at once in sea-water, 50 per cent. floated after three weeks, and 10 per cent. after twelve weeks. Of seeds that had been kept three years, 50 per cent. floated after eleven weeks. The seeds are to be found in numbers amongst the stranded drift of the Fijian and Ecuador beaches, and I noticed them also afloat in the Rewa estuary of Fiji.

I tested the floating-power of the seeds of C. sericea in Fiji, and found that half of them remained afloat after sixty days. On the seeds of C. ensiformis I have not experimented; but their buoyancy is indicated by the frequent occurrence of the plant on the Solomon Island coral islets (Guppy's *Solomon Islands*, pp. 290, 292, 296), and probably the Canavalia seeds identified at Kew from my drift collections on these islets belong to this species. Schimper (p. 166) refers to the seeds of a Canavalia in Java that were still afloat after ten weeks. These littoral plants are indebted for the floating capacity of the seed to the buoyant kernel.

NOTE 55 (page 42 and Note 20)

The Inland Extension of Scævola Kœnigii

Scævola sericea (Forst.), a hairy variety of this littoral plant, will probably prove in some localities to be the inland form of the species. Dr. Reinecke, who mentions only this variety for Samoa, says that it is found in very moist ground in river-ravines, and no other station is referred to. It would seem that both the glabrous and hairy forms occur in Hawaii. Dr. Seemann speaks of the hairy variety as littoral in Fiji.

NOTE 56 (page 149)

On the Capacity for Dispersal by Currents of Sophora tomentosa, S. chrysophylla, and S. tetraptera

(1) *Sophora tomentosa, Linn.*—The moniliform pods will float for few weeks, but it is to the seeds liberated by the breaking down of

the pod that the wide dispersal of this beach-plant by the currents is due. When experimenting on the freshly obtained seeds in Fiji I found that four-fifths of them floated after three months in sea-water. With seeds that had been kept for three years, half floated after twelve months and retained their sound condition. The seeds owe their floating power to the buoyant kernel.

(2) *Sophora chrysophylla*, *Seem.*—The dry pods of this Hawaiian mountain species float between one and two weeks in sea-water, but being brittle they readily break down and the seeds escape. The seeds have no buoyancy even after drying for four years.

(3) *Sophora tetraptera*, *Ait.*, from the coast of Chile.—After floating from ten to fourteen days in sea-water, the dry pods become sodden and begin to break up, the seeds escaping. Since, however, the pods tend to decay and break open on the tree they would not be available for dispersal by currents. Out of a number of freshly gathered seeds all floated buoyantly after a month in sea-water, when the experiment ended; and of seeds that had been kept over a year six out of ten floated after four months in sea-water, two of them germinating afterwards in soil. Like those of S. tomentosa the seeds possess buoyant kernels to which the floating power is due. On account of the hardness of the tests the seeds to ensure rapid germination require to be filed.

NOTE 57 (page 153)

On the Species of Ochrosia

Schumann distinguishes the following species:

(*a*) O. parviflora, Hensl., widely spread in the Pacific islands.

(*b*) O. compta, Schumann, confined to Hawaii and corresponding to var. B. of O. sandwicensis as given by Hillebrand.

(*c*) O. borbonica, Spr., synonym O. oppositifolia, Lam., from Mauritius and Madagascar to Java and Singapore.

(*d*) O. sandwicensis, Gray, of Hawaii.
O. elliptica, Lab., of New Caledonia. } Both probably varieties of O. borbonica.

(*e*) O. parviflora, Schumann, of New Guinea, probably identical with O. mariannensis.

NOTE 58 (page 156)

On Pandanus (from Warburg)

(a) *The size (length) of the drupes of endemic species in oceanic islands.*—The drupes of P. reineckei of Samoa are 4–5 cm. ($1\frac{3}{5}$–2 inches). Those of P. joskei and P. thurstonii in Fiji measure respectively 6 cm. ($2\frac{2}{5}$ inch) and $2\frac{1}{2}$ cm. (1 inch).

Out of about sixteen species in the Mascarene Islands (Mauritius, Réunion, and Rodriquez) quite half have drupes 2–$3\frac{1}{2}$ cm. ($\frac{4}{5}$–$1\frac{2}{5}$ inch)

in size, whilst they run up to 8 or 10 cm. (3–4 inches), and may be less than a centimetre ($\frac{2}{5}$ inch).

(b) *The affinities of the Fijian and Samoan species.*

P. odoratissimus	Wide-ranging	Section Keura.
P. joskei	Fiji	,, Lophostigma.
P. samoensis	Samoa	,, Lophostigma.
P. thurstonii	Fiji	,, Acrostigma.
P. reineckei	Samoa	,, Hombronia.

NOTE 59 (page 188)

Seeds in Petrels

Darwin, in his correspondence (1859) with Sir Joseph Hooker, refers to the occurrence of large West Indian seeds in the crops of some nestling petrels observed by Sir William Milner at St. Kilda (*Life and Letters*, II, 147, 148). Mr. Charles Dixon in *Ibis* (1885) refers to Sir W. Milner's observation in the case of the Fulmar Petrel (Procellaria glacialis) and speaks of them as Brazilian seeds brought by the Gulf Stream, adding that he himself found a nut in the crop of one of these birds in the same locality. He supposes that the birds pick them up from the water. Mr. Hemsley very kindly wrote to Sir Joseph Hooker recently on this point with the object of obtaining some idea of the nature of the seeds; but after this lapse of time it has not been found possible to satisfy my curiosity. I live in the hope of their proving to be Cæsalpinia seeds.

NOTE 60 (page 202)

Schimper on the Halophilous Character of Littoral Leguminosæ and of Shore Plants generally

As a result of extensive microchemical investigations, this eminent German botanist arrived at the conclusion that plants living on the sea-shore, or in inland stations rich in chlorides, are able, as a rule, to store up in their tissues a large quantity of these salts, a capacity enabling them to live in localities where the subsoil is rich in these materials. This inference, as shown in his experiments, is just as applicable to the shore-plants of temperate regions, such as Aster tripolium, Crambe maritimum, and Eryngium maritimum, as it is to such typical littoral plants of the tropics as Barringtonia speciosa, Ipomea pes capræ, Scævola Koenigii, Tournefortia argentea, &c. However, with the Leguminosæ experimented upon, this capacity of storing up chlorides was often exhibited but slightly or not at all; and characteristic Pacific beach-plants, such as Canavalia turgida, Pongamia glabra, and Sophora tomentosa are especially cited as examples (Schimper's *Ind. Mal. Strand-flora*, pp. 140–151; Wolff's ash-analyses are here quoted).

NOTE 61 (page 215)

Meteorological Observations on the Summit of Mauna Loa

The summit is formed of bare rock and sand, the phanerogamic vegetation ceasing a couple of thousand feet below. Some low plant-forms doubtless occur under the moist, warm conditions near the steam-cracks, since Wilkes mentions his finding a small moss; but with this exception the surface may be described as sterile.

Dryness of the Air and Electrical Phenomena.—Wilkes refers to the association of these conditions more than once in his narrative. Whenever, as sometimes happened, the dew point could not be obtained with Pouillet's hygrometer, electricity was easily excited, and was developed in large sparks. On taking off the clothes at night, sparks would appear. As shown in the table subjoined, electrical phenomena were noticed during the first few days of my sojourn on the summit when the relative humidity was very low. My red blanket at night crackled in my hands and emitted sparks, and a glowing line was produced by drawing the finger along. Whilst the air was in this condition I observed that the wings of dead butterflies lying on the ground stuck to my fingers tenaciously like a needle to a magnet. The adhesiveness disappeared when the excessive dryness gave place to humidity. The physiological effect on me of the associated dryness and electrical state of the air was displayed in a hot, dry, sweatless skin (cracking and chapping rapidly), severe headache and sore-throat, general lassitude, and great irritability. When the weather changed and the air became humid, these unpleasant symptoms quickly disappeared.

As a result of these dry conditions on the summit of Mauna Loa, decomposition does not occur. I found in one place on the top, on the site of an old camp, the remains of a quarter of beef, the meat fresh but dried up. From a water-bottle left behind by one of the party and subsequently restored to him, I learned that the visit had been made in the previous summer. This non-decomposition seems a little strange, since, as remarked below, flies and other insects were not infrequent on the summit. However, as Hann remarks, when speaking of mountain climates, everything dries much more quickly at great altitudes; animals that have been shot, or killed by falling, become mummies without undergoing decay (Schimper's *Plant-Geography*, 697). . . . The scorching power of the sun in a sky usually cloudless, or nearly so, was a trying feature of my daily experiences; and I found that when I faced it with unshaded eyes during my walks I suffered from severe pain in the eyeballs at night.

Insects on the Summit.—It may seem a strange thing to relate, that in a region apparently absolutely sterile, the flies and other winged insects caused me much discomfort in my small tent when I was confined to it through illness. When lying down one morning I noticed the house-fly, the blue-bottle, and two or three other flies, small beetles not over a fifth o

an inch in size, a moth, and a wasp. They were no doubt quite happy in the heat, as the temperature inside was over 80° F., and the sun's rays felt almost scorching through the thin duck canvas. Butterflies (and occasionally large moths) were often observed flying in a drowsy condition about the summit and were easily caught. They were fond of fluttering around the steam-holes. In places, numbers were to be seen dead and dried up on the ground, the detached wings lying about. In the case of a recently dead butterfly I found its carcase already attacked by numerous small bugs. The butterflies were most frequent when there was a fresh southerly breeze, and were doubtless blown up the slopes from the forests below.

Whymper in his *Travels amongst the Great Andes of the Equator* gives many particulars of the occurrence of insects at great elevations. He noticed beetles, diptera, butterflies, moths, and several other insects at altitudes of 15,000 to 16,000 feet. At 16,500 feet he obtained a small bug of the genus Emesa. He quotes Humboldt and Bonpland as showing that insects are transported into the upper regions of the atmosphere 16,000 to 19,000 feet above the sea, and he remarks that the transportation of insects by ascending currents of air has occasionally been observed in operation. These facts bear directly on the dispersal of insects.

The Winds.—My tent, which was pitched near the middle of the western border of the crater, happened to be situated in the battle-ground of the northerly and southerly winds, in a region of gusty winds, fitful airs, and dead calms. The northerly winds were usually from N.–N.N.W. and the southerly winds from S.W.–S.S.W., easting in either case being rarely observed, the northerly winds rather prevailing at night. As a result of this location miniature whirlwinds were frequent in the vicinity of my tent, which carried sand into the air and more than once threatened to lift up my tent bodily and carry it off into the crater below. At the north end of the crater-border north-easterly winds prevailed, and at the south end southerly winds occasionally showing easting. When on one occasion I walked round the crater-margin, a fresh south-easterly wind prevailed at most parts of the circumference except in the vicinity of my camp, where there was a light S.S.W. wind both at 8 a.m. and 6 p.m. when I started and returned. The local character of the winds was often displayed in my walks. On one occasion, having left my camp, where a southerly wind was blowing, and walked half a mile to the north, I found a bitterly cold N.N.E. gale in my face which so impeded my progress that I returned to my camp where the same southerly breeze continued.

Commodore Wilkes was encamped on the east side of the crater, and there (December and January) he experienced strong south-west winds, on at least three days having the force of a gale. These are the prevailing winds in this season over the group; whereas in August, the time of my sojourn, south-westerly winds are quite out of season, this being in the midst of the period of the N.E. trades.

It will be gathered from the foregoing remarks that the mere record of

the winds is insufficient for the purpose of obtaining any definite notion of the air-currents at this elevation (13,600 feet). It is to close observation of the clouds that we must look for data of importance.

The Clouds.—The clouds on the summit of Mauna Loa were an unending source of interest to me, and I will give briefly the results of my observations. The highest clouds were wispy cirri, often arranged as in a mackerel sky, and evidently at a great altitude. They were only observed on four or five days. (The lower clouds are indicated in the accompanying diagram.) Below them and at no great height above the mountain were to be not infrequently observed isolated woolly clouds that were carried in a few minutes across the sky and had a brief existence, often forming and melting away as one gazed at them. Next, there was a heavy bank of cumulus, which formed on the south-west slope near the top of the mountain, from which lines of cloud extended along each flank. Lowest of all was a broad belt, or rather a sea, of cumulus that was developed on both sides of the mountain about one-third way down its slopes, and during the day-time isolated the peak from the world below. It is with the last two cloud formations that we are most concerned, and I will first describe the sea of cumulus.

The sea of cumulus, as in the case of similar cloud-formations of most other isolated mountains, when viewed from above, as from the mountain-top, presents a cloud-field of dazzling whiteness, sparkling in the sun. Seen from below, as from the coast, it has the dark lowering appearance of the rain-cloud and indicates the rain-belt. Disappearing during the night, this broad belt begins to form again between 8 and 9 a.m., and by 10 or 11 a.m. the lower regions are completely hidden and the mountain's summit, cut off from the world, rises above the level of the sea of clouds like an island in an Arctic ocean. As the day progresses the clouds become more compact and dense. The usual altitude of this broad belt of cloud is between 7,000 and 8,000 feet. This level is indicated by the burying of the Kohala mountains, which rise to a height of 5,500 feet in the distant north-west corner of the island, and by the usual emergence of the highest summit of Hualalai, which rises, still nearer, to an elevation of 8,275 feet. On some days, however, it attains a height of nearly 9,000 feet. On such occasions the highest peak of Hualalai kept reappearing and disappearing during the day, but the distant summit of Haleakala in East Maui, 10,032 feet in elevation and 80 miles away, was always visible.

Words fail to describe the magnificent aspect of this sea of cloud which shuts off the spectator from the world below. From the summit of the mountain he gazes down on its surface lit up by a sun shining in a typically cloudless sky. At one time it appears as an undulating Arctic land covered with snow of dazzling whiteness. At another time it looks like a hummocky frozen Polar sea sparkling in the sunshine. Through occasional rifts, however, one can discern a dark dismal region of mist and rain-cloud beneath. Miss Bird, who passed a night on the summit in June, 1874,

[To face page 585.

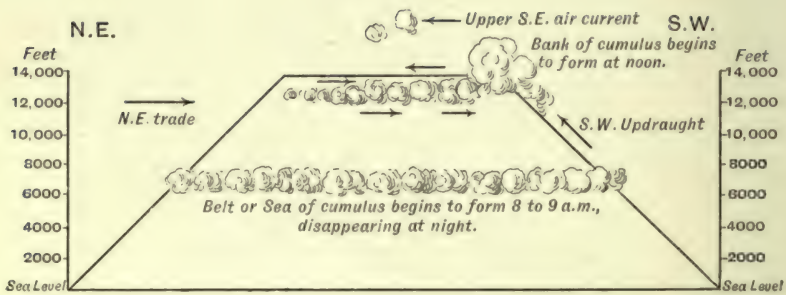


Diagram illustrating the prevailing cloud-formations of Mauna Loa during August, 1897.

well describes this sea of cloud in her book on the Sandwich Islands as "all radiance above and drizzling fog below."

The heavy bank of cumulus, that forms at noon on the south-west slope at an altitude of 10,000 to 13,000 feet above the sea, and sometimes rises above the mountain, is one of the most conspicuous of the cloud-phenomena on the summit of Mauna Loa. Apparently extending from it, but in reality moving towards it, are two lines of small cumuli that follow the same level along either flank above the sea of cumulus, as is indicated in the accompanying diagram. It was observed by Wilkes in mid-winter, 1840–41, but at a lower level. "Clouds would approach us (he writes) from the south-west when we had a strong north-east trade wind blowing, coming up with their cumulus front reaching the height of about 8,000 feet, spreading horizontally and then disappearing." During my sojourn this bank formed a very striking feature in the landscape during the early afternoon. On two or three occasions when I visited the south side of the summit and descended for about a thousand feet I passed through this bank, being then exposed to a driving mist coming up the slopes from the south-west. Though its upper surface viewed from a distance is dazzling white, below it is dark and nimboid.

It is to an updraught of warm moist air on the south or south-west slopes of the mountain, and to the prevailing cool north-east trade that strikes the north side of the summit, that we must look for the explanation of the development and situation of this bank. Although the trade-wind is markedly stronger than the south-west updraught, some of the warm, moist, southerly air-currents find their way, as shown by the observations at my camp, along the sides of the summit, and a line of condensation is produced where they come into contact with the cool air of the north-east trade as it sweeps past the flanks of the mountain. Sometimes at my camp, when there was a light southerly breeze blowing, I have noticed the line of small cumuli moving south along the mountain side towards the bank of cumulus. . . . I may remark that on a few days a small bank of cumulus formed under similar conditions on the north-west side of the summit.

From my study of the clouds I arrived at the conclusion that there were three prevailing air-currents on the summit of Mauna Loa:

(1) The updraught of warm moist air on the south and south-west slopes of the mountain.

(2) The north-east trade wind, the upper limit of this air-current being probably not far above the summit.

(3) An upper air-current from the south-east (E.S.E.—S.S.E.), which, from the velocity of the clouds it carried, was often probably not over a couple of thousand feet above the summit. It may be observed that on the coast at the base of the southern slope of the mountain in the middle of September, when the wind was N.E. and carried the lower clouds with it, the upper clouds were, on several occasions, noticed travelling in the opposite direction, namely, from the south.

The volcano was quiescent during my visit and could have exercised but little influence on the air-currents.

The Shadow of the Mountain.—Every morning and evening, in clear weather, for about twenty minutes after sunrise and before sunset, the shadow of the mountain was thrown back against the sky of the opposite horizon. It seemed as if some Titanic brush, at work in the sky far away, had painted in the profile of the mountain with a very uncanny blue. At sunset the peak was the last to disappear. Commodore Wilkes, who only records it once, namely, at sunset on the 1st of January, describes it as "a beautiful appearance of the shadow of the mountain projected on the eastern sky . . . as distinct as possible, its vast dome seemed to rest on the distant horizon." This phenomenon is, of course, well known in the case of other isolated mountains. According to Murray's *Handbook of Southern Italy* (1892), the correct thing for a visitor to Stromboli is to make an early ascent of the cone to observe "the very curious triangular shadow of the mountain cast by the rising sun upon the *sea*." Unfortunately I neglected my opportunity when on the island. The shadow of the mountain is also one of the sights of Etna, a dark-violet, triangular shadow (Baedeker) being thrown at sunrise over the surface of West Sicily, that is, on the *land*. I saw the shadow but imperfectly outlined, as the weather was not favourable at the time of my ascent. When at Nicolosi, on the south slope of Etna, I noticed at sunset a faint shadow of the mountain thrown against the eastern sky. I gathered from a short conversation with Prof. Ricco, the director of the Catania Observatory, when I told him of the shadow of the Hawaiian mountain, that the interest lay in its projection against the sky. It is doubtless akin to the spectre of the Brocken and other mountain spectres.

Some Previous Meteorological Observations on Mauna Loa.—. . . Mr. Douglas, the botanist, who was subsequently found dead in a cattle-pit on Mauna Kea, spent a day on the summit of Mauna Loa in the middle of January, 1834. He mentions that a little way below the top the thermometer fell at night to 19° F. The wind on the top was N.W. The air at 11.20 a.m. was 33°, the hygrometer registering 0·5. He remarks that the great dryness of the air was evident without the assistance of the hygrometer (*Hawaiian Spectator*, vols. I and II, 1838–9).

Commodore Wilkes, in vol. IV of his *Narrative of the United States Exploring Expedition*, gives the following observations on the temperature and winds on the top of Mauna Loa between Dec. 23, 1840, and Jan. 13, 1841. Those on the temperature are incomplete, but they give a fair idea of the prevailing conditions. The degrees are in Fahrenheit's scale.

Dec. 23, 1840: elevation, 13,190 feet; 3 p.m., 25° F.; strong S.W. gale; night temperature, 15°.
„ 24, „ summit (13,600 feet); night minimum, 22°.

Dec. 26, 1840:	summit (13,600 feet);	violent S.W. gale; night min., 17°.
„ 27, „	„ „ „	sunrise temp., 20°; night min., 17°; wind, S.W.
„ 29, „	„ „ „	noon temp. in shade, 47°; night min., 20°.
„ 30, „	„ „ „	noon temp., 55°; night min., 13°.
„ 31, „	„ „ „	night min., 17°.
Jan. 2, 1841:	„ „ „	sunrise, 20°; wind, N.E.
„ 3, „	„ „ „	night min., 17°.
„ 4, „	„ „ „	daylight, 20°.
„ 8, „	„ „ „	S.W. gale.
„ 10, „	„ „ „	night temp., 16°.
„ 12, „	„ „ „	night temp., 17°.
„ 13, „	„ „ „	strong S.W. wind.

The usual variation of temperature in the twenty-four hours is given as 17°—50°. The south-west was evidently regarded as the prevailing wind, and the clouds are spoken of as sometimes moving from opposite directions towards the same centre.

When Miss Bird spent a night on the summit of Mauna Loa during the eruption of June, 1874, the cold was described as intense, eleven degrees of frost (21° F.).

Observations on the Summit of Mauna Kea.—. . . When Prof. Alexander with a party of scientists ascended this mountain (in the summer of 1892), the thermometer at night fell to 13° F., and the trade-wind was found to be blowing as strongly on the summit as down below (Whitney's *Tourist Guide to Hawaii*). It is to be inferred that the party camped by the small lake which is a few hundred feet below the actual summit (13,800 feet). This lake, which I visited on May 20, 1897, is about 120 yards across, and evidently shallow, probably not more than three or four fathoms deep. A carpet of algæ covered the bottom. At noon, by the lake, the air in the shade was 53° F., whilst the temperature of the surface-water was 51°. The lower clouds were moving from S.S.E. This lake is said to be permanently frozen over in the winter, and to have been visited by skaters.

Permanent Water Supply on the Summit of Mauna Loa.—In this barren rocky region water derived from the winter-snow is to be found all the year through at the bottom of the deep cracks or fissures in the lava-rock. Such fissures are from two to four feet wide, and in the case of that near my tent the bucket had to be lowered to a depth of seventeen or eighteen feet to reach the water, or rather the ice, since it was often necessary to break the surface ice. In these deep, narrow fissures, which the sun scarcely penetrates, the water would probably be frozen over all through the seasons; but in those of less depth it would remain liquid in summer.

REGISTER OF OBSERVATIONS ON WIND, RELATIVE HUMIDITY, CLOUD, RAIN, AND TEMPERATURE, MADE BY H. B. GUPPY ON THE SUMMIT OF MAUNA LOA AT AN ELEVATION OF 13,500 FEET ABOVE THE SEA, AUGUST 9TH TO 31ST, 1897. (CAMP ABOUT MIDDLE OF WEST SIDE OF CRATER MARGIN)

Date.	Observation.	12—4 A.M.	4—8 A.M.	8—12 A.M.	12—4 P.M.	4—8 P.M.	8—12 P.M.	Air in shade.			Remarks.
								Min.	Max.	Range.	
9	Wind	S.S.W.—S.W. 2	Variable	...	W.S.W.—W.N.W. 3	N.N.W.–N. 1	N.N.W.–N. 3	F.	F.	F.	A beautifully coloured lunar halo at 1 A.M. Electrical condition of the atmosphere (see text).
	Rel. hum.	...	...	...	...	...	...	27·5	61·2	33·7	
	Cloud	0	0	0	0	0	0				
	Rain	0	0	0	0	0	0				
10	Wind	...	N.N.W. 2	S.S.W—W.S.W. 3	S.S.W.—W.S.W. 2	Calm	...				Electrical condition of the atmosphere. Faint lunar halo at 8 P.M.
	Rel. hum.	...	...	34	42·5	46	...	33·5	59·7	26·2	
	Cloud	...	0	1	2	0	...				
	Rain	0	0	0	0	0	0				
11	Wind	Calm	W.S.W. 1	...	...	S.S.W.—S.W. 1	...				Electrical condition of the atmosphere.
	Rel. hum.	...	...	{28·5 21	...	...	...	22·5	61·2	38·7	
	Cloud	0	0	0	1	0	...				
	Rain	0	0	0	0	0	0				
12	Wind	Calm	Calm	N.N.W.—N. 2—3	N.N.W. 1	N.N.W.—N. 2—4	N. 2—4, S.W.—W.S.W. 3—5				Earth tremors. Total rain, $\frac{20}{100}$. At sunset, wind N.W., wet canvas of tent froze hard. At 10 P.M., strong southerly wind, canvas thawed, rain with strong gusty wind until 4 A.M., when wind less.
	Rel. hum.	...	...	45	79	89	...	23	54·7	31·7	
	Cloud	0	0	5	10	10	5				
	Rain	0	0	0	Rain	Rain	Rain				
13	Wind	S.W. 4—6	S.W. 3—5	S.W.—S.S.E. 3—4	S.W. 3	Calm; N.W. 1	...				Earth tremors. Total rain $\frac{10}{100}$.
	Rel. hum.	...	...	86	86	78	...	33·6	48·7	15·1	
	Cloud	...	10	7	10	9	...				
	Rain	Rain	Rain	0	Rain	Rain	0				
14	Wind	N.N.W.–N. 1	Northerly, 3	N.N.W. 3	N.N.W. 2	N.N.W. 1	...				Butterflies flying about in a semi-torpid state, and easily caught with the hand.
	Rel. hum.	...	61·5	47	42	45·5	...	32·5	52·2	19·7	
	Cloud	3	0	0	0—2	0	...				
	Rain	0	0	0	0	0	0				
15	Wind	Northerly, 1	W.S.W. 1, N.N.W. 1	S.W.—W. 2	Calm; Southerly, 1	Calm; N.N.W. 1	N.N.E.—1—2				Wind fitful during day; north-westerly and south-westerly airs with calms.
	Rel. hum.	...	...	38	44·5	{62 52·5	...	28	54·7	26·7	
	Cloud	0	0	0	7	7—0	0				
	Rain	0	0	0	0	0	0				

Date.	Observation.	12—4 A.M.	4—8 A.M.	8—12 A.M.	12—4 P.M.	4—8 P.M.	8—12 P.M.	Air in shade.			Remarks.
								Min.	Max.	Range.	
16	Wind	Calm	N.N.W. 2	N. 3	...	Southerly, 1	...				Carefully observed the shadow of the mountain which, at sunrise and sunset, is projected against the opposite horizon.
	Rel. hum.	...	...	{32, 28}	...	61	...	26	53·2	27·2	
	Cloud	...	0	0	7	0	...				
	Rain	0	0	0	0	0	0				
17	Wind	...	N.N.W. 1	N.N.W. 2, Southerly, 2	N.-N.N.E. 3, Southerly, 2	N.N.W. 1	...				Fitful northerly and southerly winds causing miniature whirlwinds that carried dust and paper up into the air.
	Rel. hum.	...	...	32	32·5	...	...	20·5	58·7	38·2	
	Cloud	...	0	0	1	0	...				
	Rain	0	0	0	0	0	0				
18	Wind	Calm	S.W. 1	Variable	...	S.W. 2	...				—
	Rel. hum.	...	...	26	...	47	...	23	58	35	
	Cloud	0	0	0	1	0	...				
	Rain	0	0	0	0	0	0				
19	Wind	...	...	N.N.W. 1, W.S.W. 1	Northerly, 3, S.S.W. 3	Northerly, 2, Southerly, 2	Southerly, 3				Through the day, fitful northerly and southerly breezes.
	Rel. hum.	...	...	20	23	{24, 35·5}	...	22	58·7	36·7	
	Cloud	...	...	0	0	0	0				
	Rain	0	0	0	0	0	0				
20	Wind	Southerly, 2	Northerly, 1, Southerly, 1	Northerly, 1, Southerly, 1	S.S.W.—S.W. 4	Northerly, 2, Southerly, 1	Southerly, 3				Fitful northerly and southerly airs, often reversing several times in a few minutes.
	Rel. hum.	...	...	26·5	25	29·5	...	22	57·2	35·2	
	Cloud	0	0	0	0	0	0				
	Rain	0	0	0	0	0	0				
21	Wind	Southerly, 4	Southerly, 3-4	S.S.W. 3—4	S.S.W. 4—5	S.W. 4—5	S.W. 4				At camp, strong southerly winds all day. At 7 A.M., walked half-mile north and found a bitterly cold N.N.E. gale blowing there, which forced me to return to camp where the south wind still blew freshly.
	Rel. hum.	...	...	35·5	31	47	...	26·5	53·7	27·2	
	Cloud	...	0	0	0	0	...				
	Rain	0	0	0	0	0	0				
22	Wind	...	S.S.W. 1	...	...	Calm, Southerly, 2	...				Walked round the crater from 8 A.M. to 6 P.M.
	Rel. hum.	...	...	58	...	...	...	20·5	46·7	26·2	
	Cloud	...	0	0	1	0	...				
	Rain	0	0	0	0	0	0				
23	Wind	...	S.S.W. 2	...	N.N.W.—N.E. 1—3, Southerly, 3	Southerly, 1	Calm				A few drops of rain at 2 P.M.
	Rel. hum.	...	...	{60, 54·5}	{52·5, 64}	70	...	24	50·7	26·7	
	Cloud	...	0	3	3—8	3—6	0				
	Rain	0	0	0	Rain	0	0				

REGISTER OF OBSERVATIONS ON WIND, RELATIVE HUMIDITY, CLOUD, RAIN, AND TEMPERATURE (*continued*)

Date.	Observation.	12—4 A.M.	4—8 A.M.	8—12 A.M.	12—4 P.M.	4—8 P.M.	8—12 P.M.	Air in shade.			Remarks.
								Min.	Max.	Range.	
24	Wind	...	Northerly, 3	S.W. 1	N.N.W.—N. 2—3	N.N.W.—N. b. E. 2-3	Northerly 2				
	Rel. hum.	...	...	54·5	...	53	...	20	52·7	32·7	
	Cloud	...	0	0—1	4	0	...				
	Rain	0	0	0	0	0	0				
25	Wind	Calm	...	Calms with N.W. and S.W. airs	Calms with N.W. and S.W. airs	Northerly and Southerly airs	Northerly and Southerly airs				A few drops of rain at 3 P.M.
	Rel. hum.	...	...	{42·5 37·5}	{73·5 61·5}	61	...	17	52·2	35·2	
	Cloud	0	0	0—1	2—9	0	0				
	Rain	0	0	0	Rain	0	0				
26	Wind	Northerly, 2	N.N.W. 1	...	N.N.W.-N. 3	N.N.W. 2	...				Descended through the bank of cumulus on S.W. slope and found driving mist coming up the slope from S.W.
	Rel. hum.	...	...	49·5	...	64	...	19·5	53·7	34·2	
	Cloud	0	...	3	3	0	0				
	Rain	0	0	0	0	0	0				
27	Wind	Calms with light airs	Calms with light airs	S.W.—W.S.W. 2	W.S.W.-W. 1	Southerly	Calm				Rain not measurable. Rain-clouds poured into and filled the huge crater.
	Rel. hum.	...	...	35	73·5	...	...	18·5	50·7	32·2	
	Cloud	0	0	4	10	4	0				
	Rain	0	0	0	Rain	0	0				
28	Wind	Calms with northerly airs	Calms with variable airs	N.N.W.—N. 2—3	S.S.W. 3	Northerly, 3	Calms with variable airs				9 A.M., high stationary cirrus; at noon, solar halo; in afternoon, nimbus partly filling crater causing a rainbow there; a few drops of rain at 4 P.M.
	Rel. hum.	...	...	{46·5 59·0}	{64·5 73·0}	...	...	15	49·7	34·7	
	Cloud	0	0	5	7	0	0				
	Rain	0	0	0	Rain	0	0				
29	Wind	N.N.W.-N. 3	N.N.W.-N. 2	N.—N. b. E. 3	N.N.W. 3, S.S.W. 2	Calms with variable airs	Northerly, 1				
	Rel. hum.	...	...	45	44	60·5	...	21·5	48·7	27·2	
	Cloud	0	0	0	0	0	0				
	Rain	0	0	0	0	0	0				
30	Wind	Calms with northerly airs	Southerly, 1	N.N.W. 2—3	N.N.W. 3	Calms with variable airs	...				
	Rel. hum.	...	...	32·5	{41·0 54·5}	...	...	18	50·7	32·7	
	Cloud	0	0	0	0	0	0				
	Rain	0	0	0	0	0	0				
31	...	...	...	...	...	...	...	18·5	50·0	31·5	

Method of Observation employed by the Author on the Summit of Mauna Loa.—My camp was placed near the middle of the west margin of the crater about 13,500 feet above the sea. The instruments employed were a Sixe's maximum and minimum thermometer made by Negretti and Zambra, several unmounted thermometers, and a reference thermometer (with a Kew certificate) by the above-named makers, which was used as a standard. The freezing point was also tested for all the instruments on the summit in melting powdered ice. The maximum air observations and those on the relative humidity were taken in a small cave with a hole in the roof, through which there was a steady flow of air. One day was occupied in comparing the cave-observations with those obtained under a temporary screen rigged up outside my tent, the only difference shown being as a rule less than a degree. The minimum observations taken in my tent, where there was no artificial heat, were usually only 1·5° higher than those given by a thermometer outside the tent.

Results of the Observations on the Top of Mauna Loa, Aug. 9–31, 1897

Mean minimum temperature of air in shade	23·2° F.
Mean maximum " " "	53·8°
Mean daily range of temperature	30·6°
Lowest reading	15·0°
Highest reading	61·2°
Mean temperature for the period	38·5°

Mean relative humidity, 8—9 a.m.,	44·5 °/₀	Many observations included which are not given in the register.
" " " noon ...	43 °/₀	
" " " 5—6 p.m.,	56 °/₀	

On Aug. 11th, at 10 a.m., wet bulb, 33·2°; dry bulb, 52°; difference, 18·8°.

On Aug. 19th, at 11 a.m., wet bulb, 35·7°; dry bulb, 56°; difference, 20·3°.

Owing to the varying winds at my camp, the relative humidity fluctuated greatly in a short time. Thus, on Aug. 12 it was 46 °/₀ at noon, and 79 °/₀ at 2 p.m.

Average Cloudiness (10 *indicating a Sky completely Overcast*)

12—4 A.M.	0	Cloudless during 12 out of 13 days
4—8 "	0	" " 19 " 20 "
8—12 "	1·3	" " 13 " 22 "
12—4 P.M.	3·5	" " 6 " 22 "
4—8 "	1·5	" " 17 " 22 "
8—12 "	0	" " 11 " 12 "

The winds at the camp were extremely variable and local from north and south, usually light, with force 1–3: see under Winds and Clouds in the text.

Rain fell on six days, total $\frac{30}{100}$ of an inch: but on four of the days it was not measurable.

NOTE 62 (page 222)

On the Relative Proportion of Vascular Cryptogams in Fiji

According to Seemann's work, where about 617 indigenous flowering plants and about 195 ferns and lycopods are enumerated, the vascular cryptogams would form about 24 per cent. of the whole flora. (All weeds and cultivated plants are here excluded.) The vascular cryptogams, however, seem to figure too prominently in Seemann's collections. From Horne's data, who says that he added 363 flowering plants to the flora, the flowering plants would amount to about 980; and since Baker implies, in *Trimen's Journal of Botany*, 1879, that Horne added 42 species of ferns and lycopods to the flora, this would increase the vascular cryptogams to 237, which enables us to estimate the relative proportion of vascular cryptogams in Fiji as about 20 per cent. of the whole flora of vascular plants. This is probably near the truth.

NOTE 63 (page 222)

On the Table of Vascular Cryptogams of Tahiti, Hawaii, and Fiji

In the case of Tahiti, I have gone carefully through the list given by Drake del Castillo, comparing it with other Polynesian lists given by Seemann, Horne, Hillebrand, Hemsley, &c., and have reduced his endemic species from 19 to 13. The same thing has been done with Hillebrand's list for Hawaii, some of his species having been found in other parts of Polynesia, thus reducing the endemic species from 75 to 70. The data relating to Fiji are referred to in Note 62.

NOTE 64 (page 223)

On the Distribution of the Tahitian Ferns and Lycopods

I have arranged them as follows, according to the distributions given by Drake del Castillo:—Cosmopolitan, 5; Tropics of Old and New Worlds, 33; Tropics of Old World, mainly Indo-Malaya, 58; "Océanie," including Australia, 17; Polynesia, 26; South America, 2; peculiar to Tahiti, 13: total, 154.

Out of 141 non-endemic Tahitian species, 107 at least have been recorded from the Fijian area comprising Samoa and Tonga, and 42 from

Hawaii. Of the last, all but four occur also in Fiji. There is thus a very small element peculiar to Hawaii and Tahiti alone. Some of them will no doubt be found in the Fijian area; whilst two of them, Acrostichum squamosum and Lycopodium venustulum, are high-mountain forms in Hawaii and Tahiti, which have evidently failed to find a suitable elevation in Fiji.

NOTE 65 (page 225)

DISTRIBUTION OF SOME OF THE MOUNTAIN FERNS OF HAWAII THAT ARE NOT FOUND EITHER IN FIJI OR TAHITI (mainly from Hillebrand)

Species.	Altitude of station in feet.	General distribution.
Schizæa robusta, Bak.	3,000—6,000	Perhaps a form of S. australis, Gaud., from the Falkland and Auckland Islands.
Polypodium serrulatum, Mett.	3,000—6,000	Generally diffused in the tropics and sub-tropics.
Aspidium caryotideum, Wall.	In the forests	Himalayas, South Africa, &c.
,, filix mas, Sw.	In the highlands	Over four continents, from the arctic circle to the higher levels of tropical mountains.
Asplenium trichomanes, L.	5,000— 8,000	Temperate zones and the higher levels of tropical mountains.
,, monanthemum, L.	3,000— 6,000	American Andes, Madeira, Tristan d'Acunha, Azores, Abyssinia, &c.
,, fragile, Presl.	4,000— 6,000	Andes.
,, contiguum, K.	2,000— 5,000	Lord Howe Island, Ceylon, Neilgherry Hills.
,, adiantum nigrum, L.	4,000—10,000	Europe, Asia, Africa, Atlantic Islands.
,, aspidioides, Sch.	1,000— 6,000	Andes, Africa, India.

NOTE 66 (page 226)

ENDEMIC GENERA OF FERNS IN HAWAII

Hillebrand gives two genera of ferns peculiar to Hawaii, one, Sadleria of Kaulfuss, "scarcely distinct from Blechnum," and containing four species; the other, Schizostege, constituted by himself, and represented by a single species found in only one or two of the islands.

NOTE 67 (page 241)

ON THE DISPERSAL OF COMPOSITÆ BY BIRDS

The goldfinch's habit of pecking at the heads of thistles, and pulling out the achenes in bundles, is well known. Gätke mentions two suggestive instances of birds feeding on the fruits of a Composite plant. According to this observer, the Scarlet Grosbeak (Pyrrhula erythrina), when it alights on Heligoland, always feeds on the achenes of Sonchus oleraceus, which it picks off the plant; whilst the Parrot Crossbill (Loxia sp.), feeds in Heligoland on burrs and thistles (*Heligoland as an Ornithological Observatory*, pp. 407, 409). See Note 91.

NOTE 68 (page 264)

On some of the Hawaiian Endemic Genera, excluding those of the Compositæ and Lobeliaceæ

Haplostachys, Phyllostegia, and Stenogyne, all Labiate Genera.—Phyllostegia is not strictly peculiar to Hawaii, since out of the 17 species enumerated in the *Index Kewensis*, 15 are Hawaiian, 1 Tahitian, and 1 is accredited to Unalaska (one of the Aleutian Islands). The last locality appears to be an error. The species in question is P. microphylla, Benth.; and on looking up the original authority in *Linnæa* (vi. 570, 1831), I find the locality is thus given: "insula coralligena Romanzoffii," which is either one of the atolls of the Paumotu Islands in about lat. 15° S. and long. 144° W., or a coral island of the Marshall Group, most probably the former. . . . I paid some attention to the suitability of the fruits of these three Labiate genera for dispersal by frugivorous birds, for which the fleshy nucules in the cases of Phyllostegia and Stenogyne apparently fit them. Out of the fruits of five species of Phyllostegia examined by me, the seed-coverings in three species, after the removal of the fleshy covering of the nucule, were too soft for the protection of the seed in a bird's stomach. Hillebrand also observes (p. 347) that the nucules when dried are wrinkled, and absorb moisture easily, a quality which, if true of all the species, would make the distribution of the genus by birds impossible. However, in two species I found the seed-coverings somewhat harder. It would seem that since birds have largely ceased to disperse these plants, the soft-skinned nucules would in the absence of their selective agency more frequently characterise the genus. It is possible that the dry nucules of Haplostachys, which according to Hillebrand are not affected by drying, represent the original condition of those of Phyllostegia, and that the fleshy character has been acquired in this archipelago. It will be seen in the list on page 263, that Haplostachys is regarded by Gray as a section of Phyllostegia. The remarks under Phyllostegia, regarding the softness of the seed-coverings beneath the fleshy coat of the nucule, also apply to Stenogyne; and Hillebrand, in contrasting its fleshy nucules with the dry nucules of Haplostachys, implies that they absorb water, which, I may remark, would render them quite unfit for dispersal by frugivorous birds.

Touchardia (*Urticaceæ*).—According to Hillebrand, the solitary species is by no means common in the group now. In 1897 I found it growing abundantly some miles up the Waipio gorge, Hawaii.

Cheirodendron (*Araliaceæ*).—C. Gaudichaudii, the well-known "Olapa" tree, is common in the forests of all the Hawaiian Islands between 2,000 and 5,000 feet; but I noticed it occasionally at greater elevations, as on the south-east slopes of Mauna Kea, where it extends to 7,000 feet. As described on page 343, the "Olapa" often grows in close contact with the Lehua (Metrosideros polymorpha), the two trunks appearing as one. The

drupes would attract frugivorous birds and the pyrenes are well adapted for this mode of dispersal. Mr. Perkins states that the drupes are much sought after by the various species of Phæornis, a genus of birds peculiar to Hawaii.

Deterioration of Fruits for Purposes of Dispersal.—Among fruits of endemic genera that have evidently deteriorated in the Hawaiian Group as far as fitness for dispersal is concerned, may be mentioned, in addition to those of Phyllostegia and Stenogyne above noticed, those of the Araliaceous genera, Pterotropia and Triplasandra, and the Amarantaceous Nototrichium. The pyrenes of the first two genera on account of their thin covering, and the seed of the last-named genus on account of its thin testa, seem ill-fitted now for transport in a bird's stomach, yet we cannot doubt that their ancestors originally arrived in this fashion. The same principle is also illustrated by some Hawaiian non-endemic genera of later eras that possess peculiar species, such, for instance, as in the case of Elæocarpus discussed in Chapter XXVI.

NOTE 69 (page 366)

On the Germination of Cuscuta

My observations were made on the Hawaiian endemic species (C. sandwichiana) and on a Fijian introduced species. Germination occurs readily in fresh water, the floating seedling growing rapidly. When the germinating seed is placed on wet soil in the shade, the seedling grows at the rate of ¾ inch (19 mm.) a day. The store of nutriment contained in the swollen radicular end will support the seedling for a couple of days, and if it has not then found a host it withers and dies. At first lying prone the seedling then lifts its upper end into the air, and it was almost pathetic to notice it moving round and round, endeavouring vainly to find some object near. The seedlings make no effort to strike into the soil, and when they are allowed to attach themselves to a plant they ascend rapidly, growing at the upper end and dying at the lower end.

NOTE 70 (pages 477, 480-1)

On Beach-Temperature

My data are rather scanty; but, judging from observations made in Hawaii, in South America, and in the south of England, the following scale would probably be true of typical beaches where the sand is found relatively cool and moist at a depth of four or five inches. This moisture seems to arise entirely from subsoil drainage seaward. When a beach fronts an arid, rainless region, few if any plants grow on it; the sand is loose, hot, and dry at the depth indicated; and the temperature of the surface half-inch rises to between 130° and 140° F., whilst four inches down

it is 95° to 100°. Salt-marshes situated behind a beach even in a desert-region change its thermal behaviour, and it would then be more like a beach skirting a vegetated sea-border in the same latitude. The method of observation was as follows :—An unmounted thermometer of the size of a clinical thermometer, but graduated higher, was placed horizontally in the sand half an inch below the surface and a reading taken. It was then pushed vertically into the sand until the bulb was four inches deep and another reading taken. Provided that the sand is moist beneath, the colour does not seem to make much difference, except perhaps in very dark sands, none of which were tested.

Ordinary Beach-Temperatures with an Unclouded Sky in the Hot Season during the Early Afternoon.

	Surface half-inch.	Four inches deep.
Temperate latitudes about 50—55°	100—105° F.	77° F.
Sub-tropical ,, ,, 30—35	105—110	80
Tropical ,, ,, 10—20	110—120	85

This illustrates only the average condition. On a calm day in the case of a beach facing south in the South of England, I have obtained exactly the same readings in July as at Valparaiso in January, 112° at surface, 80° four inches deep.

NOTE 71 (page 479)

On the Buoyancy of the Seeds or Seed-vessels of some Chilian Shore Plants

(1) *Nolana*, probably *paradoxa*. Common on the beaches of Southern Chile. The ripe drupes have a somewhat fleshy outer covering which they lose when lying on the sand, and present themselves then as dark-brown angular "stones," often five to six millimetres across. Inside the outer hard covering of the stone is a layer of spongy tissue which gives it buoyancy; but since these coverings are wanting at the scars marking the basal insertion of the drupe, the embryo seems insufficiently protected against injury during flotation in sea-water; and the seed-vessel at first appears to be only fitted for conveyance by the currents over a limited tract of sea. However, in a preliminary experiment on seed-vessels that had been kept a few weeks, I found that 30 per cent. floated after three weeks in sea-water. Subsequently, after drying for a year, the seed-vessels were again tested in sea-water, nearly all of them floating after three months' immersion. Two of them, removed after six weeks' flotation, germinated healthily. These fruits are common in beach-drift between Corral and Valparaiso.

(2) *Raphanus*, near R. maritimus. Growing near beaches in South

Chile, and not infrequently represented in the stranded beach-drift by the pods, which in my experiments floated seven to ten days in sea-water, after drying some weeks.

(3) *Franseria*. A species common on the beaches of Valparaiso and Talcahuano. Its prickly fruits, after being kept six weeks, floated only two to four days. They are well suited for transport in birds' plumage.

NOTE 72 (page 483)

The Southern Limit of the Mangrove Formation in Ecuador. . . . The southern limit of the mangrove formation on the west coast of South America is usually placed at 4° S. lat.; but it is probable that the vicinity of Tumbez in lat. 3° 30′ S. would be more correct. Baron von Eggers would place it rather further to the north-east, near the frontier of Ecuador and Peru in lat. 3° 20′ S. I spent eight days in the locality last named and saw no evidence of the beginning of the mangrove-formation.

NOTE 73 (page 495)

Additional Note on the Temperature of the Dry Coast of Ecuador between Puna Island and the Equator. . . . Baron von Eggers gives the mean annual temperature for El Recreo, about half a degree south of the equator, at 75° F., which is near that of Rio de Janeiro in lat. 23° S. on the east coast of the continent. Mr. F. P. Walker has kindly given me the results of temperature-observations covering a period of ten years, taken in the room for testing cables at Santa Elena Point (2° 10′ S.), usually about 6·30 a.m. The range of the monthly means was 71° F. (August) to 79·1° (March), and the mean for the year was 74·8°. In that locality a typical daily range would be 65° to 80°; and Mr. Walker believes that a minimum of 59° has been recorded.

NOTE 74 (page 495)

Observations on the Temperature of the Humboldt Current from Antofagasta Northward, between January and March, 1904 (Fahrenheit scale)

The observations were usually taken at the anchorages, but in some places, as at Ancon and Puerto Bolivar, they were taken from a boat outside the roadstead.

If we wish to ascertain how the Humboldt Current retains its cool temperature as it advances through the tropics to the equator, a glance at the following table will show that the surface-temperatures can aid us but slightly, since they do not vary in accordance with the latitude, a subject further discussed below. We can, however, obtain some valuable indications from the deeper temperatures. Let us take for

instance the plane of 60°. Whilst south of Ancon (lat. 11° 45′ S.) it was rarely deeper than four fathoms, north of this latitude it descends rapidly, being probably about ten fathoms down at Salaverri and Eten and about twenty fathoms deep at Payta, in latitude 5° S., where the Humboldt Current leaves the coast. Within the Gulf of Guayaquil it is probable that the plane of 60° would descend to nearer thirty fathoms, the region being outside the influence of the current.

Some interesting facts are also elicited from the variation of the surface-temperatures. When we were coasting along at a distance of five or six miles from shore the readings were fairly constant from hour to hour varying only a degree or so. But nearer the land, for instance, about two or three miles away, the variation from hour to hour amounted to two or three degrees, whilst within the limits of the anchorages, a mile and less from the coast, the change from hour to hour amounted to three or four degrees. Nor was there any uniformity at the same hour over the surface of a roadstead. The temperature would often rise or fall a degree every few boat-lengths. Sometimes the inshore water was the coolest and sometimes it was the warmest. Thus at Iquique the inshore water was three degrees warmer than the water half a mile out, whilst at Mollendo, when the temperature one-third of a mile off the shore was 70°, it was 63° close to the rocky coast. The same thing was exhibited at Pisagua, where the surface-water two miles out at sea was 61°, whilst close inshore at the anchorage it was 58°. It was evident that there was a considerable intermingling of the warmer surface and the colder, deeper waters on the coasts of Chile and Peru. This was particularly noticeable on a rocky, steep-to coast, or where there was an uneven bottom. At some places, indeed, the warm upper layer did not exist, the cold water welling up all along the coast. This was especially the case between the 22nd and 19th parallels of latitude, a tract of coast in which lie Tocopilla, Iquique, and Pisagua, and probably the coolest part of the sea-border at this season of the year.

During a fortnight spent at Ancon (11° 45′ S.), between January 27 and February 10, I paid considerable attention to the local climatic conditions, and especially to the temperature of the inshore water. The daily range of the air-temperature was only five or six degrees, the average minimum and maximum being 71° and 75·9°, and the mean for the period 73·5°. The mean temperature of the surface-water at the head of the pier, from observations taken at about 7 a.m. and 4 p.m., was 68·6°, or five degrees cooler than the air, the mean temperature in the morning being 69·1° and in the afternoon 68°.

The Ancon climate at this period is full of oddities and abnormalities, and in this way typifies much of the coast of Peru. Thus, since the heat of the day is tempered by the cool south-westerly winds which die away in the evening and give place usually to warm, light, northerly and north-westerly breezes, there is, as above remarked, but a small difference between

Observations on the Temperature of the Humboldt or Peruvian Current

(Made by H. B. Guppy, January to March, 1904. Those at Panama are added for the sake of comparison)

Locality.	Depth (fathoms).	Distance from shore (miles).	S. lat.	Date.	Hour.	Depths in fathoms : temperature in Fahrenheit degrees.																						
						Surface.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.
Antofagasta	22	3/8	23°40′	Jan. 12	5 p.m.	71°	70°	...	...	...	...	...	61°	...	...	57°	...	...	...	...	...	56°	...	...	...	...	...	...
				,, 13	6 a.m.	70	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	55	...	...
Tocopilla	18	1/2	22 0	,, 14	8 a.m.	57	...	...	...	...	...	...	...	...	...	56	...	...	...	...	...	55	...	...	...	...	...	...
Iquique	9	3/8	20 15	,, 15	5.30a.m.	59	...	...	...	...	58	...	...	...	55	...	...	...	...	...	...	...	...	...	...	...	...	...
Pisagua	10	1/2	19 30	,, 16	8 a.m.	57·5	...	...	..	...	...	...	...	...	...	56	...	...	...	...	...	...	...	...	...	...	...	
Arica	...	1/4	18 25	,, 16	7 p.m.	66	...	...	...	...	...	...	...	57	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Mollendo	22	1/8	17 0	,, 17	8 a.m.	61·5	...	...	...	...	...	...	...	57	...	...	...	...	...	...	..	...	...	...	...	...	...	...
			,,	,, 17	6 p.m.	65	...	...	...	...	...	...	...	...	...	59	...	...	...	...	...	...	...	...	...	...	...	...
			,,	,, 18	9.30a.m.	62	...	...	...	...	57·5	...	...	...	...	57	...	...	...	...	56	...	...	...	...	...	...	55
Callao	5	1	12 3	,, 20	6 a.m.	60·5	...	...	...	...	58·5	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Ancon	17	1 3/4	11 45	,, 29	11 a.m.	66	...	...	6·15	...	58·5	...	..	57	...	57	...	...	...	...	...	...	56·5	...	...	...	...	...
Salaverri	6	3/4	8 15	Febr. 21	6.30p.m.	65	...	...	...	...	...	62	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Eten	7	1/2	7 0	,, 22	8 a.m.	66·5	...	...	...	...	...	...	63	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Payta	16	1 1/2	5 0	,, 23	9 a.m.	70	...	..	...	...	...	...	67·5	...	...	...	...	...	...	...	62·5	...	...	...	...	...	...	...
Puerto Bolivar	10	1	3 10	Mar. 7	noon	78	...	...	...	...	71·5	...	...	...	...	70	...	...	...	...	...	...	...	...	...	...	...	...
Panama	8	3	(8 50 N.)	,, 23	4 p.m.	82	...	...	...	...	...	...	79·5	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
				,, 24	7 a.m.	79·5	...	...	...	...	...	...	...	79.5	...	...	...	...	...	...	...	...	...	...	...	...	...	...

day and night temperatures. The coldest time of the twenty-four hours is not in the early morning but at sunset. The sea off the beach is, on the average, much cooler than the air, which is not a normal state of things; and again, the water is often two or three degrees colder in the evening than it is in the morning, which is very unusual. Though the sea-border is practically a desert for the greater part of the year and has no rain, it is frequently enveloped in drizzling fogs or "garuas." Judged from a European standard, things go by contraries on the coast of Peru; and this is entirely the effect of the Humboldt Current.

The temperature of the inshore waters of Ancon Bay varied considerably during the twenty-four hours. During the day, with the prevailing southerly wind, the cool waters of the current had free access to the bay, and swept around its border in their course north; but in the night, when northerly breezes occurred, the cold waters of the current were pushed off the coast and their place taken by the warmer inshore waters from the north; and this sometimes continued for a day or two. When the current again got mastery and its clean, cool waters filled the bay, the temperature of the water dropped suddenly five or six degrees, and the bay was filled with fish. At such times men in boats leave the beach, and in a few minutes, with hand-nets and baskets, they obtain thousands of the small fry. Other men, fishing with lines from the pier-head, seem ill-contented unless they can catch fish of the size of small mackerel at the rate of one a minute.

There can be little doubt that on the coasts of Chile and Peru the instincts of fish often lead them astray, on account of the sudden changes of temperature arising from the conflict between the warmer waters of the open sea and the cooler waters of the current. From the preceding remarks it will be inferred that sometimes the current is pushed off the coast for a while and its place taken by the warm waters from the north. At other times it dives down, so to speak, and flows at a deeper level, and warmer waters prevail both out at sea and inshore. At other times again, and this must be most disconcerting to the fish, the cold current suddenly appearing at the coast predominates at the surface for days together, and we have stretches of coast which, although lying within tropical latitudes, are washed by waters having the temperature of the temperate zone. It is to such causes that we must attribute the reckless habits of fish on these coasts. They are known to throw themselves on the beaches in thousands, where by their decay they taint the air long afterwards. Mr. Anderson Smith in his recent book on *Temperate Chile* vividly describes what goes on on such occasions at the port of Valdivia. At times the scene must be indeed a strange one, since huge octopi are rolled up on the beaches in numbers, and are regarded by the indigenes as deliberately seeking their death. Whether they commit suicide or not, "their beaks that blacken the edge of the sea-wash in places" afford a melancholy proof that their instinct has blundered.

The Mode of Observation.—A thermometer made on the Sixe pattern which I used several years ago for taking the bottom-temperatures of rivers, was employed for the deeper temperatures, and at critical depths the observations were always repeated. This instrument was compared after each set of observations with an ordinary thermometer graduated on the stem, which was compared with my standard thermometer provided with a Kew certificate. . . . The observations in the Panama Roadstead have been added for the sake of contrast.

NOTE 75 (page 496)

On the Stranded Massive Corals apparently of the Genus Porites found on the Coast of Peru and North Chile, at Arica (18° 25′ S.), Callao (12° 3′ S.), and Ancon (11° 45′ S.)

At Arica they occurred on the beach only. At Callao they also extended inland on the low spit at Punta for about 100 yards. At Ancon they were found not only on the beach but also twenty or thirty paces inland on the low adjoining plains. Their size varied from three inches to three feet. They were all more or less rounded by wave action, and were extensively burrowed by boring molluscs. Whilst some on the beach still displayed the dried-up soft parts of the boring mollusc, others inland were falling to pieces and undergoing chemical change. There was nothing to indicate that the corals were recently alive; and at Ancon they appeared to have been torn off a rocky spit of andesite that had become exposed on the beach during a recent movement of emergence, of which there is other evidence on this coast. Further particulars are given on page 496.

NOTE 76 (page 429)

Stranded Pumice on English and Scandinavian Beaches

Sernander, in his description of the Atlantic drift of the Scandinavian coast, refers to the occurrence of a small amount of true pumice. I have found solitary fragments of acid pumice well rounded by wave-action at Croyde Bay on the north coast of Devonshire, at the mouth of Salcombe Harbour on the south coast of the same county, and at Maenporth, near Falmouth, in Cornwall. Steamer slag, in some cases rudely simulating pumice, is common on all the South of England beaches I have examined. It is also common on the Scandinavian coasts, though seemingly regarded by Helge Bäckström, who is quoted by Sernander, as derived from the factories on the east coast of England. (See on these subjects a paper by Helge Bäckström, "Über angeschwemmte Bimsteine und Schlacken der nordeuropäischen Küsten"; Bihang till *K. Sv. V. A. Handl.* Bd. 16. Afd. 3, 1890; also a letter in *Nature*, about 1886, by H. B. Guppy.)

NOTE 77 (page 21)

On the Mode of Dispersal of Kleinhovia hospita

This small tree has a very wide distribution in the tropics, ranging from East Africa and the Mascarene Islands through India, South-eastern Asia, Malaya, New Guinea, and the Solomon Islands to Fiji and Tahiti. It is a plant that grows in inland open woods as well as amongst the littoral trees on the beach; and it is always doubtful (in Malaya, Fiji, and Samoa) whether to regard it as a shore plant or as an inland plant, different authors varying on this point. In Vanua Levu I formed the opinion that it is only an intruder amongst the littoral vegetation. In accounting for its distribution we have to choose between man, the bird, and the current. Though it may sometimes be noticed in native plantations, as I observed in the Solomon Islands, the tree has no special use; and the Solomon Island natives themselves indicated to me that the parrots that fed on the fruits of the tree aided in distributing the plant. The buoyant behaviour of the seeds, which are freed by the dehiscence of the bladder-capsules on the tree, is not constant. Whilst in the case of the seeds of littoral trees in Fiji I found that 30 per cent. floated after ten weeks, Prof. Schimper ascertained in the case (seemingly) of Malayan seeds that they sank at once. The seed-structure connected with the buoyancy is, as shown on page 105, accidental in character, and reference is made on page 20 to other plants of doubtful littoral reputation, in which the buoyant qualities are variable. The occasional buoyancy of its seeds will only, as I think, explain its occasional station at the coast; and I agree with Prof. Schimper (p. 156) when he attributes its wide distribution to birds, the seeds being hard, crustaceous, and about three millimetres across.

NOTE 78 (page 436)

On the "Sea": an Unidentified Wild Fruit-tree in Fiji

This is a fair-sized forest tree common in places in the lower forests. I have never been able to identify it; but a "putamen" which was sent to the Kew Museum was named Spondias with a query. It is to be hoped its true botanical name will be discovered by one of my successors. Seemann places it amongst the "desiderata" concerning which further information is needed. The fruit is a drupe 2 to $2\frac{1}{2}$ inches long possessing a pleasant fruity odour and inclosing a hard two-celled stone about $1\frac{2}{3}$ inch long, one cell containing a large fleshy seed covered with tawny hair, the other filled with the hair only and containing no seed. The Fijians say that these fruits, large as they are, are swallowed by the fruit-pigeons, the stones being found in their gullet. The leaves are distichous, alternate, lanceolate, eight or nine inches long, glabrous and dark green above, and covered below with a whitish woolly matted tomentum. The empty stones are not uncommon in the stranded beach-drift.

NOTE 79 (page 395)

On Willow-leaved River-side Plants

A number of observers, beginning with Humboldt, in his *Ansichten der Nature*, and including Seemann, L. H. Grindon, Ridley, Beccari, and others, have referred to what is called "stenophyllism" in plants. These willow-leaved river-side plants are found all over the globe, such plants usually growing close to the water's edge in situations where they are liable to be more or less submerged when the river is in flood. Seemann, Beccari, and Ridley mention more than two dozen genera belonging to a great variety of orders, and including Acalypha, Antidesma, Calophyllum, Eulalia, Eugenia, Fagræa, Ficus, Garcinia, Ixora, Lindenia, Melastoma, Podocarpus, Psychotria, &c., all tropical, and represented either in Fiji, Borneo, or in the Malay Peninsula; whilst my readers will recall amongst temperate floras river-side plants of the genera Epilobium, Lythrum, Salix, &c., possessing the same form of leaf and the same station. The genus Eugenia comes under this category in Fiji, Borneo, and the Malay Peninsula, with reference to one or more of the species. In Fiji, species belonging to the genera Lindenia and Dolicholobium especially attracted my attention in this respect. It is noteworthy that several of the Bornean plants and some of the Fijian plants here concerned are endemic. Just as I have remarked in the question of the buoyancy of seeds and fruits, that not all water-side plants have buoyant seeds or fruits, but that nearly all plants thus endowed are found at the water-side, so we may say of the willow-leaved plants, that not all river-side plants have the willow-form of leaf, but that plants thus characterised gather at the river-side. Beccar and Ridley regard this willow-form of leaf as the result of adaptation. Seemann remarks that we have here the old question whether the webbed feet of a duck are the cause or the effect of the bird's swimming; and I take the same position. (See Seemann's *Flora Vitiensis;* Ridley in *Trans. Linn. Soc. Bot.*, vol. iii. 1888–94; and Beccari's *Nelle Foreste di Borneo*, 1902, or the English edition of 1904.)

NOTE 80 (pages 255, 504)

Mr. Perkins on the Hawaiian Lobeliaceæ (*Fauna hawaiiensis*, vol. I.)

My view, that the early Hawaiian Lobeliaceæ acquired the monstrous form of their flowers in the humid forests of a later age, is supported by the observations of Mr. Perkins on the connection between the highly-specialised nectar-eating Drepanids of Hawaii and the highly-specialised flowers of the Tree-Lobelias, a subject further discussed in Chapter XXXIII. This naturalist ascertained, in the case of one of the trees, that fertilisation could only be effected by these birds. So close is the biological connection

between the Drepanid and the Tree-Lobelia, that Mr. Perkins finds here in part the cause of the development of the most remarkable forms of the birds. The botanist, also, would not dissociate the plants from this conclusion. There would be every reason to look for abnormal growth in birds and plants when the bird depends on the flower for its food, and the flower is dependent on the bird for its pollenisation. It is through such guises that the zoologist and the botanist have to penetrate when establishing the systematic affinity.

NOTE 81

On the Vertical Range of some of the most Typical and most Conspicuous of the Plants in the Forests on the Hamakua Slopes of Mauna Kea, Hawaii

During a descent of this mountain on its north side to near Ookala, the conditions were unusually favourable for recording the range of altitude for some of the plants easily recognisable.

Acacia koa began at 6,700 feet, and extended down to 2,300 feet.

Rubus ("akala") began at 6,500 feet, and extended down to 2,500 feet.

Cheirodendron ("olapa") began at 6,400 feet, and extended down to 2,200 feet.

Cyanea, a lobeliad growing on trunks of tree-ferns, began at 4,000 feet, and extended down to 2,300 feet.

Freycinetia began at 3,850 feet, and extended down to 2,000 feet.

Asplenium nidus began at 2,800 feet, and extended down to 2,200 feet.

Aleurites moluccana began at 1,800 feet, and extended down to 50 feet.

Metrosideros polymorpha, ranging through all the zones.

NOTE 82 (page 416)

Aboriginal Weeds[1]

(Found by Captain Cook's Botanists, Banks, Solander, the Forsters, Nelson, &c., in the Pacific Islands, 1768–80)

	Locality given by Cook's botanists.	General distribution.
Cardamine sarmentosa	Tahiti	Polynesia. Introduced into Peru.
Sida microphylla	Tonga, New Hebrides	Old World tropics.
Sida rhombifolia	New Hebrides. H.	Tropics of Old and New World.
Urena lobata	Tahiti	Tropics of Old and New World.
Waltheria americana	Tahiti. H. New Caledonia	Tropics of Old and New World.
Oxalis corniculata	Tahiti	Old and New World.

[1] Seemann is the principal authority, the results of his examination of the old collections being given in his *Flora Vitiensis*. Species regarded by Hillebrand as indigenous in Hawaii or as existing in that group at the time of its discovery by Cook are indicated by H in the second column.

ABORIGINAL WEEDS (*continued*)

	Locality given by Cook's botanists.	General distribution.
Cardiospermum halicacabum	Tahiti. H.	Tropics of Old and New World.
Desmodium polycarpum	Tahiti	Old World.
Phaseolus truxillensis	Tahiti. H.	Tropics of Old and New World.
Lablab vulgaris	Tahiti	Old World tropics.
Abrus precatorius	Tahiti	Tropics of Old and New World.
Cassia sophora	Tonga	Tropics of Old and New World.
Hydrocotyle asiatica	New Caledonia	Tropics of Old and New World.
Oldenlandia tenuifolia	New Hebrides	Old World?
Oldenlandia paniculata	Tonga	Old World tropics.
Geophila reniformis	Tahiti	Tropics of Old and New World.
Ageratum conyzoides	New Hebrides. H.	Tropics of Old and New World.
Adenostemma viscosum	Tahiti. H.	Tropics of Old and New World.
Eclipta alba	New Hebrides	Tropics of Old and New World.
Siegesbeckia orientalis	Tahiti	Tropics of Old and New World.
Bidens pilosa	Tonga	Tropics of Old and New World.
Dichrocephala latifolia	Tahiti, Tonga, New Hebrides	Old World tropics.
Sonchus asper	Tonga, New Zealand	Old World.
Ipomea insularis	New Hebrides, Tonga, Hawaii	Australia and Polynesia.
Ipomea bona-nox	New Hebrides, Tonga, Tahiti. H.	Tropics of Old and New World.
Solanum nigrum, var. oleraceum.	Tahiti. H.	Old and New World.
Physalis angulata	Tahiti	Tropics of Old and New World.
Vandellia crustacea	Tahiti	Tropics of Old and New World.
Leucas decemdentata	Tahiti	Old World tropics.
Teucrium inflatum	Tonga	New World tropics.
Amarantus melancholicus, var. tricolor	New Hebrides, Tahiti	Old World.
Euxolus caudatus	Tonga, Tahiti	Old World tropics.
Achyranthes aspera	Tahiti	Old and New World.
Cyathula prostrata	Tahiti	Old World tropics.
Fleurya interrupta	Tahiti, Tonga	Old World tropics.
Commelina pacifica	Tonga, New Caledonia. H.	Tropics of Old and New World.
Eleusine indica	Tahiti. H.	Tropics of Old and New World.

NOTES 83—89 omitted

NOTE 90 (page 29)

ON THE BUOYANCY OF THE SEEDS OF EUPHORBIA AMYGDALOIDES AND E. SEGETALIS

The seeds of both species have no proper buoyancy, and display no structure in their testas suggesting it; though, through the shrinking of the nucleus, a temporary floating power may be acquired with less mature or imperfect seeds. They support the general principle indicated for the British species on page 29.

NOTE 91

MR. E. KAY ROBINSON ON THE DISPERSAL OF ASTER TRIPOLIUM

According to this naturalist, the seeds of this plant are eaten in winter by snow-buntings on the English east coast. In reply to my query he tells me that the "draggled fluff still containing seeds" might easily adhere to birds (*The Country-Side*, Sept. 30, 1905).

GENERAL INDEX

Note.—Several subjects are worked up in this index, which, on account of the plan of the book, are not dealt with connectedly in the text. As examples may be cited the entries under the heads of "Hawaiian Flora"; "Species, their development"; "Fruit-pigeons"; "Polymorphous Species"; &c.

The figures in larger type indicate the pages where the subject is treated at length or where the most important points are discussed. This sign is not often used where the references can be classed, or where several references of importance belong to the same subject.

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